Duke University Libraries
D02280137N

DUKE
UNIVERSITY

LIBRARY

Digitized by the Internet Archive
in 2019 with funding from
Duke University Libraries

https://archive.org/details/factorsinfluenci00zobe

Duke University Library

The use of this thesis is subject to the usual restrictions that govern the use of manuscript material. Reproduction or quotation of the text is permitted only upon written authorization from the author of the thesis and from the academic department by which it was accepted. Proper acknowledgment must be given in all printed references or quotations.

FORM 412 1M 11-43

FACTORS INFLUENCING THE DISTRIBUTION OF *PINUS PUNGENS*, AN APPALACHIAN ENDEMIC

by

Donald Bruce Zobel

Department of Botany
Duke University

Date: April 16, 1968

Approved:

W.D. Billings, Supervisor

A dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany in the Graduate School of Arts and Sciences of Duke University

1968

FACTORS INFLUENCING THE DISTRIBUTION OF *PINUS PUNGENS*,

AN ARVIDSONIAN ENDEMIC

by

Donald Bruce Zobel

Department of Botany
Duke University

Date: _____

Approved:

_____
W.D. Billings, Supervisor

_____

_____

_____

_____

A dissertation submitted in partial fulfillment
of the requirements for the degree of Doctor
of Philosophy in the Department of Botany
in the Graduate School of Arts and
Sciences at Duke University

1963

Frontispiece: *Pinus pungens*, Table Mountain pine, at 2600 feet on Kate's Mountain, Greenbrier County, West Virginia. The large tree, 20 inches diameter and about 65 feet tall, shows a common form with long, heavy limbs on the downhill, exposed side of the tree. The small tree, left foreground, has many serotinous cones along the trunk. A small *P. virginiana* is in the center foreground.

Frontispiece: *Pinus pungens*, Table Mountain pine, at 2600 feet on Kate's Mountain, Greenbrier County, West Virginia. The large tree, 20 inches diameter and about 65 feet tall, shows a common form with long, heavy limbs on the downhill, exposed side of the tree. The small tree, left foreground, has many serotinous cones along the trunk. A small *P. virginiana* is in the center foreground.

ABSTRACT

(Botany)

FACTORS INFLUENCING THE DISTRIBUTION OF *PINUS PUNGENS*, AN APPALACHIAN ENDEMIC

by

Donald Bruce Zobel

Department of Botany
Duke University

Date: April 16, 1968

Approved:

W.D. Billings

W.D. Billings, Supervisor

H. L. Oosting

Paul J. Kramer

Donald E. Stone

K. R. Knoerr

An abstract of a dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Botany in the Graduate School of Arts and Sciences of Duke University

1968

Th.D.
Ph.D.
1964

ABSTRACT

Factors Influencing the Distribution of *Pinus pungens*, an Appalachian Endemic

Pinus pungens Lambert, Table Mountain pine, has a limited range in the Appalachian Mountains. East of the mountains it occurs sporadically on monadnocks or near major rivers. Herbarium specimens and personal collections were used to define the geographic range. Environmental comparisons were made of forest stands with *P. pungens* and those without the species. Physiological studies of seeds and seedlings and phenological observations were used to evaluate hypotheses explaining relationships found in the field. *Pinus pungens* was compared primarily to *P. virginiana* and *P. rigida*, generally sympatric with *P. pungens* but much more common and with wider ranges. Intraspecific variation of some morphological and physiological characteristics of *P. pungens* was investigated.

Pinus pungens occurs in small stands from Pennsylvania and New Jersey to Georgia, usually at elevations of 1000 to 4000 feet (305 to 1220 meters). Stands commonly occur on exposed sites with a south to west aspect, areas with the warmest, driest microclimate. In the Valley-and-Ridge

province, this pine often occurs on shale outcrops. Soils on which it grows are shallow, rocky, and acid, and have lower nutrient levels than neighboring stands without the species.

The most permanent stands of this species are associated with a greater amount of rock outcrop and shallower litter than the more temporary stands. The species is most often associated with Quercus prinus, Q. coccinea, Pinus rigida, and P. virginiana. Signs of fire are present in almost all stands. Squirrels (presumably Tamiasciurus hudsonicus) eat seed stored in the serotinous cones and cut off the ends of branches.

Cone length, width, length:width ratio, and seed weight of Pinus pungens decrease with elevation. Needle length:width ratio and cone scale number are highest in the southern part of the range. Height of two-year-old potted seedlings is inversely related to latitude of the seed source. Northern seedlings have higher transpiration rates at high soil moisture contents.

Pinus pungens makes the major part of twig growth, and releases pollen, at least as early as P. virginiana and earlier than P. rigida. Seed germinated over a narrower temperature range than P. rigida seed. Pinus pungens has larger seeds, which produce larger seedlings (in culture),

with more lateral roots and more branches, than seedlings of associated species of pine. Transpiration rates of young *P. pungens* seedlings were less than of those of *P. rigida*, and roots of very young seedlings were longer. *Pinus pungens* appears more drought resistant than *P. rigida*. Its thicker bark and serotinous cones allow stands to survive and expand in areas with frequent fires better than *P. virginiana* does.

Pinus pungens is probably excluded by low temperature or late frosts from regions or topographic situations colder than its present habitat, because of its early spring activity. Interference by other species probably excludes it from many other areas. Fire, which destroys leaf litter and competing plants, and releases stored seed, is important in allowing reproduction. Reduction in both fire incidence and abandonment of agricultural land appear to have limited recent establishment of new stands.

Further studies, especially of photosynthetic patterns and of seedling growth and survival in the field, would be useful in more closely defining factors influencing the range of *Pinus pungens*.

ACKNOWLEDGMENTS

Many people helped with this project. Sampling was done on land under the control of the following organizations, whose personnel consented to its use and provided helpful information: Pennsylvania Department of Forests and Waters; Maryland Department of Forests and Parks; Stronghold, Inc.; West Virginia Department of Natural Resources; Virginia Department of Conservation and Economic Development, Division of Parks; North Carolina Department of Conservation and Development, Division of State Parks; South Carolina State Commission of Forestry; and units of the U.S. National Park Service. Soil for experimental studies was collected by permission of the U.S. Forest Service, and many Forest Service personnel provided helpful information. John D. Barnett, Superintendent, Hanging Rock State Park, North Carolina, aided the phenological studies. The Soil Testing Division of the North Carolina Department of Agriculture did all chemical soil analyses. Dr. E.L. Little, Jr., U.S. Forest Service, and Dr. John M. Fogg, Jr., University of Pennsylvania, provided range maps upon which plans for the project were based. Dr. M.O. Braaten and Dr. J.G. Osborne, Duke University School of Forestry, gave advice regarding

statistical and computational procedures. Dr. M.R. Kaufmann assisted with the thermocouple psychrometer equipment. The interest of Dr. C.B. Davey and Dr. B.J. Zobel, N.C. State University, added greatly to the study. Anita and Kathleen Matthews enthusiastically helped harvest many of the seedling experiments. Thanks are extended to the organizations and individuals noted above, and to the many other persons who gave advice, discussion, and information which aided this project.

Guidance throughout this study provided by Dr. W.D. Billings and Dr. H.J. Oosting is greatly appreciated. Special thanks are due my wife, Priscilla, for help in the field sampling and laboratory work, and for her encouragement and understanding.

Financial support was provided by a National Aeronautics and Space Administration Traineeship from 1965 to 1967, and by a National Science Foundation Graduate Fellowship in 1967 and 1968. Support for most travel expenses was provided by National Science Foundation Research Grant GB-3698 (Billings and Oosting). Computer time and facilities were furnished by the Duke University Computation Center which is supported in part by the National Science Foundation.

Donald B. Zobel

CONTENTS

		Page
ABSTRACT		ii
ACKNOWLEDGEMENTS		vi
I. INTRODUCTION		2
II. THE DISTRIBUTION OF *PINUS PUNGENS*		8
Geographic Range	8	
Altitudinal Range	16	
Field Sampling Methods	17	
Factors Associated with *Pinus pungens*	30	
III. FACTORS DISTINGUISHING TABLE MOUNTAIN PINE STANDS FROM OAK STANDS		77
Meteorological Observations	77	
Topographic, Soil, and Vegetational Factors	81	
IV. "PERMANENCE" OF TABLE MOUNTAIN PINE STANDS		95
V. MORPHOLOGICAL CHARACTERISTICS IN NATURAL *PINUS PUNGENS*		111
Variation Patterns in Cone, Seed, and Needle Characteristics	111	
Other Species Characteristics	130	
Evidence of Hybridization	136	
VI. PHENOLOGICAL STUDIES		138
Twig Elongation	140	
Height Growth of Seedlings	146	
Needle Elongation	147	
Lateral Growth of the Trunk	147	
Time of Pollen Release	150	
Discussion	157	

		Page
VII. SEED GERMINATION STUDIES		162
Temperature-gradient Bar: Methods	163	
Preliminary Experiments	165	
Experiments G4 and G6: Species Comparisons	166	
Experiments G5, G7, and G8: Comparison of *Pinus pungens* from Different Sources	168	
VIII. PHYSIOLOGICAL RESPONSE OF SEEDLINGS		179
Water Relations	179	
Seedling Response to Increased Calcium and Magnesium	204	
Effects of Temperature	220	
Bud Formation and Growth Resumption of Seedlings	240	
Seedling Height in Relation to Source Latitude	245	
IX. DISCUSSION		249
The Environment of Table Mountain Pine Stands	250	
Environmental Factors Limiting the Distribution of *Pinus pungens*	255	
Characteristics Adapting *Pinus pungens* to Its Habitat	262	
Variation within Table Mountain Pine	267	
Conclusions	269	
X. SUMMARY		271
XI. LITERATURE CITED		276

LIST OF TABLES

Table		Page
1	Characteristics of 1965 Sampling Areas	20
2	Characteristics of Subsample Stands of 1966 Sampling Areas	21
3	Daily Potential Solar Beam Irradiation at 38° N for a 40-percent Slope	37
4	Geologic Formations on Which *Pinus pungens* Was Observed	42
5	Soil Series on Which *Pinus pungens* Was Observed in Four or More Places	44
6	Gravel over 2 mm Diameter in Soil Samples	45
7	Average Characteristics of Soils from 1966 Sampling Areas	46
8	Average Number of Higher Plant Species per Stand, 1966 Sampling Areas	49
9	Percent Presence of Tree Species in 38 Table Mountain Pine and 38 Oak Stands	51
10	Percent Presence of Shrub and Ground-cover Species in 38 Table Mountain Pine and 38 Oak Stands	52
11	Simple Correlation Coefficients and Significance in Multiple Regressions of "Value" of a Stand (Pine = +1, Oak = -1) on Site Factors	83
12	Simple Correlation Coefficients and Significance in Multiple Regressions of "Value" of a Stand (Pine = +1, Oak = -1) on Species Presence and Importance Rating	85
13	Results of Combined Regressions of "Value" on Soil and Topographic Factors	89
14	Results of Combined Regressions of "Value" on Soil and Topographic Factors and Species Presence	90
15	Results of Combined Regressions of "Value" on Soil and Topographic Factors and Species Importance Ratings	91
16	Simple Correlation Coefficients and Significance in Multiple Regressions of Stand Permanence on Topographic, Soil, and Biotic Factors	102
17	Simple Correlation Coefficients and Significance in Multiple Regressions of Stand Permanence on Species Presence and Importance Ratings	103

Table		Page
18	Results of Combined Regressions of Stand Permanence on Soil, Topographic, and Biotic Factors	105
19	Results of Combined Regressions of Stand Permanence on Soil, Topographic, and Biotic Factors and Species Presence	106
20	Results of Combined Regressions of Stand Permanence on Soil, Topographic, and Biotic Factors, and Species Importance Ratings	107
21	Comparison of Original Stand Permanence Values with Those Calculated from Combined Regression Equations	110
22	Average Needle and Cone Characters	117
23	Characteristics of Sites and Trees Used in Phenological Measurements	142
24	Characteristics and Dates for 50% and 90% Growth of Trees Used to Determine Patterns of Circumferential Increase	151
25	Observations of Time of Pollen Release	153
26	Characteristics of Soil Used for Seedlings of Experiments D and T	182
27	Soil Characteristics of Liming Experiment Soil Treatments	208
28	Selected Treatment-by-Species Means for Liming Experiment, Six-month Old Seedlings	212
29	Average Numbers of Mycorrhizae per Seedling in the Liming Experiment	214
30	Percent Survival for Liming Experiment after 13 Months	217
31	Chemical Characteristics of Limed and Unlimed Soils from the Temperature and Liming Experiments	231
32	Treatment Means for Temperature and Liming Experiment	234
33	F-values from Analysis of Variance of Temperature and Liming Experiment	236
34	Condition of Buds on Experiment D Seedlings	242

LIST OF FIGURES

Figure		Page
1	Branch of Pinus pungens	4a
2	The Natural Range of *Pinus pungens*	10
3	Moore's Knob, Hanging Rock State Park, North Carolina	13
4	Location of Sampling Areas	19
5	An Open Table Mountain Pine Stand on a Steep Shale Slope	33
6	A Contour Map of a Hypothetical 5000-foot Mountain, Showing Elevation and Aspect at the Center of 47 Table Mountain Pine Stands	35
7	Positive Correlations Found between Importance Ratings of Species Associated with *Pinus pungens*	58
8	Branches and Cones Cut by Squirrels	68
9	Cone Serotiny in 1966 Sample Areas	75
10	Vapor Pressure Deficit Difference between Pine and Oak Stands	80
11	Scatter Diagram Used to Separate Stands into "Permanence" Groupings	98
12	Average Needle Length:Width Index for Five Regions	115
13	Variation in Cone Size, Shape, and Armament	118
14	Variation of Cone Length:Width Ratio, Width, and Length with Elevation	123
15	Mean Seed Weight as a Function of Elevation	128
16	A Table Mountain Pine Showing Open-grown Form	134
17	Needle Elongation at Hanging Rock State Park, N.C.	149
18	Phenology of *Pinus pungens*, Hanging Rock State Park, Compared with Some Associated Species	156
19	Relative Germination Values (RGV) on the Temperature-gradient Bar	170
20	Peak Value and Mean Daily Germination for Species Comparisons	172
21	Peak Value and Mean Daily Germination for Comparison of Sources of *Pinus pungens*	174
22	Relationship between Water Potential of Soil and of Needles of *Pinus pungens* Seedlings	189

Figure		Page
23	Relationship between Needle Water Content and Needle Water Potential of Three Pine Species	194
24	Water Loss of Six to Seven-month Old Seedlings as Affected by Soil Moisture	200
25	Water Loss of Eighteen to Twenty-month Old Seedlings as Affected by Soil Moisture	202
26	Response of Early Seedling Growth to Soil Temperature	225
27	Response of Some Seedling Characteristics of *Pinus pungens* to Soil Temperature	229
28	Number of One-year Old Seedlings Resuming Terminal Growth by a Given Date	244
29	Height of Seedlings as a Function of Latitude of Seed Origin	247

FACTORS INFLUENCING THE DISTRIBUTION OF *PINUS PUNGENS*, AN APPALACHIAN ENDEMIC

I. INTRODUCTION

Pinus pungens Lambert, Table Mountain pine, is a hard or yellow pine endemic to the Appalachian Mountains from Pennsylvania south to Georgia, with small populations east of the mountains. It usually grows on dry, rocky or gravelly mountainsides, but occasionally occurs in moist areas in the mountains (Illick, 1928; Cooperrider & Thorne, 1964).

Although Lambert described and named the species in 1805, Andre Michaux first collected it near Tablerock Mountain in Burke County, North Carolina. Michaux made several trips through the area between 1789 and 1796, but mentions the pine only in another context (A. Michaux, 1889: p. 105). Although his statement is unclear, he seems to say the following: On February 17, 1794, in the Piedmont near Dumfries, Virginia, he found a pine which he had also seen in a cold, arid, mountainous region. Growing with this pine, in the mountains, was a second pine with recurved cone scales

with rough spines (presumably P. pungens). He states that the second pine (P. pungens, presumably) also grows on hills along the Schuyllkill River in Pennsylvania. F. A. Michaux described P. pungens briefly in 1810 and in more detail in 1819. Contrary to the elder Michaux's journal, cited above, he states (1819) that, after "extensive researches", he is sure that it is limited to "Table Mountain" and "neighboring summits". He comments that the species is likely to become extinct because of increasing settlement and frequent fires in the area.

A figure of a cone of Pinus pungens with scales and seeds dissected appeared in Lambert's (1803) "Tab. 16" with a twig of P. taeda, and was identified as the latter species because of a mixed specimen he received. Lambert (1805) corrected his mistake and described the new species from collections made by William Strickland in the "Blue Mountains" of Virginia. A branch showing the stout needles in fascicles of two, the spiny yearling cones and a maturing cone is illustrated in Fig. 1.

Several common names have been used for Pinus pungens, for example hickory pine (Sargent, 1897), prickly cone pine and poverty pine (Illick, 1928). Michaux (1810) used Table Mountain pine, the only name in use where it was first collected. The U. S. Forest Service Check List of the Trees

Figure 1. Branch of *Pinus pungens*, showing the stout needles in fascicles of two, two yearling, a second year and a mature cone. The specimen is on the tree shown in Fig. 16, at 3640 feet in Shenandoah National Park, in the central Virginia Blue Ridge.

of the United States has used this name since 1940, when it replaced the previously accepted "mountain pine" (Forest Service Tree Name Committee, 1940). "Table Mountain pine" will be used throughout this dissertation.

Pinus pungens is in the Section (or subgenus) Diploxylon, the hard or yellow pines (Shaw, 1914). Its classification below section level varies considerably. Duffield (1952) in his rearrangement of Shaw's Subsection Pinaster, places it in Group XI, with *P. caribaea* (including *P. elliottii*), *P. palustris*, *P. echinata*, *P. taeda*, *P. glabra*, *P. occidentalis*, *P. rigida*, and *P. serotina*. This is equivalent to Critchfield and Little's (1966) Group Australes. However, in Shaw's original system (Shaw, 1914), based largely on cone serotiny, it is in the Group Insignes, with only *P. rigida* and *P. serotina* of Duffield's Group XI. Pilger, relying heavily on needle number for his classification, puts *P. pungens* in Section Banksia, in which *P. echinata* is the only other species also in Group XI (Mirov, 1967).

Duffield's (1952) rearrangement is based on hybridization experiments but his placement of Table Mountain pine is due largely to its morphological similarity to *P. rigida*, which, he admits, may not be a good criterion. Hybridization of *Pinus pungens* with six species has been

attempted. P. halepensis, P. muricata, P. taeda, and P. clausa did not cross with it. Crosses with P. rigida and P. echinata were successful but difficult, and genetic barriers are considered to exist between these species and Table Mountain pine (Critchfield, 1963; Liddicoet & Righter, 1960; Duffield, 1952). Recent attempts at hybridization, in Halifax County on the North Carolina Coastal Plain, resulted in successful crosses with P. pinaster, and possibly with P. taeda and P. densiflora, as well as P. rigida and P. echinata. Crosses attempted with P. serotina, P. virginiana and P. clausa were unsuccessful (P. E. Smouse, personal communication). These results lend some support to Duffield's classification.

The range of Table Mountain pine is almost entirely within the ranges of two other hard pines, Pinus rigida and P. virginiana (Critchfield & Little, 1966). Throughout the common range of the three species, P. pungens is by far the rarest. There are large areas where it has not been reported, and, when it is present, it is usually in small populations restricted to the sites which appear least favorable for tree growth. These characteristics of habitat have caused interest in the species as a botanical curiosity and inspired romantic descriptions of the tree and its surroundings (for example, Dickey, 1926), but little scientific effort has been directed

at it. *Pinus pungens* is often a small tree, usually with poor form and large limbs, and unsuitable for many commercial uses, further limiting serious interest in it.

This study was undertaken to get detailed information about the species and its habitat, and to contribute to an understanding of the relationship between them. The purposes of the work described below were 1) to delineate the conditions where the species occurs; 2) to determine what factors differentiate the habitat of *Pinus pungens* from adjoining ones; 3) to discover, by comparative physiological experiments with seedlings of Table Mountain pine and associated species, reasons for its restricted occurrence; and 4) to discover how certain morphological and physiological characteristics vary within the species.

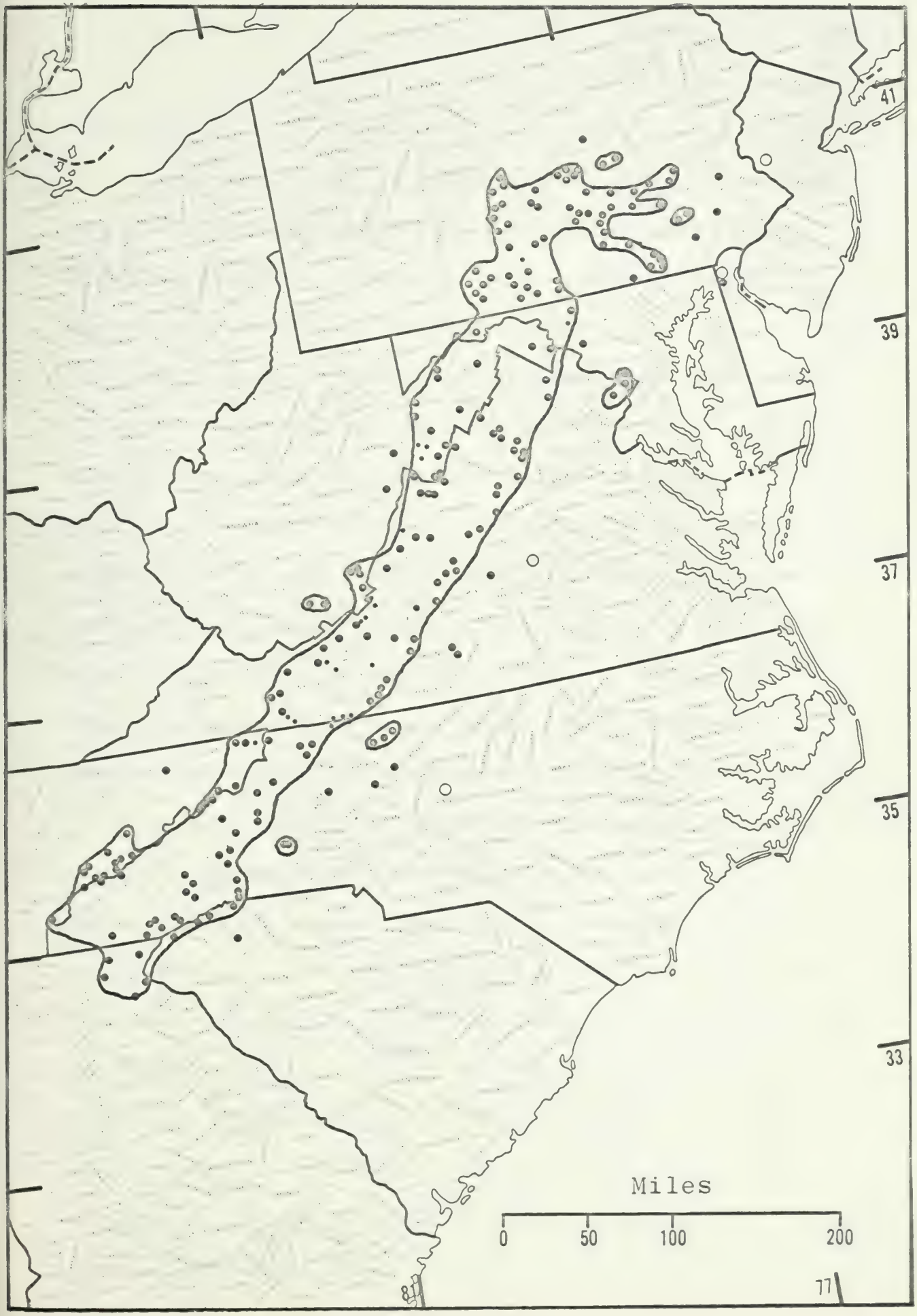
II. THE DISTRIBUTION OF *PINUS PUNGENS*

Geographic Range

Because *Pinus pungens* usually occurs in small colonies in relatively inaccessible areas, the range of the species has been hard to define. Herbarium specimens, observations, and collections made during the study were used to determine the natural range of the species. The range map in Fig. 2 was prepared using locations from personal collections and those in the following herbaria: DUKE, GA, NA, NCU, NSC, TENN, US, VPI, and WVA (Lanjouw & Stafleu, 1964). Locations for Pennsylvania supplied by Dr. John M. Fogg (personal communication) were also used.

On Fig. 2, outlying locations marked with an open circle were those visited during the study which may not be of natural origin, and at which the species is apparently not reproducing. They are discussed below. Other areas outside the main range may be in this condition but were not visited

Figure 2. The natural range of *Pinus pungens*. Larger dots are locations of herbarium specimens. Small dots are locations for which no specimens are available, but where it was observed during this study. Open circles are locations visited during the study which may not be of natural origin, and where the species is apparently not reproducing.


41
39
37
35
33
Miles
0
50
100
200
77

during the study.

The range of *Pinus pungens* is primarily in the Blue Ridge and Valley-and-Ridge provinces of the Appalachian Highlands (Fennemann & Johnson, 1946). There are numerous outlying populations to the east, however, and a few to the west. Many of the outliers are associated with monadnocks rising above the general level of the Piedmont (Fig. 3). These include Paris Mountain, Greenville County, South Carolina; the South Mountains, Burke County, North Carolina (Pinchot & Ashe, 1897); Rocky Face, Alexander County, North Carolina (Keever *et al*., 1951); Pilot Mountain, Surry County, North Carolina (Williams & Oosting, 1944); the Sauratown Mountains in Stokes County, North Carolina (Pinchot & Ashe, 1897); Smith Mountain, Pittsylvania County, Virginia; Bull Run Mountains, Prince William County, Virginia (Allard & Leonard, 1943) and Sugarloaf Mountain, Frederick County, Maryland. Other eastern range extensions are along major rivers, such as the Susquehanna in Lancaster and York Counties, Pennsylvania; the Potomac around Washington, D.C.; the James in central Virginia and the Catawba in North Carolina. The species has also been reported along the Pigg River in Pittsylvania County, and on Fork Mountain, in Franklin County, in the southern Virginia Piedmont (W. Overton, personal communication).

Figure 3. Moore's Knob, Hanging Rock State Park, Stokes County, North Carolina, a monadnock about 1700 feet above the surrounding Piedmont. Table Mountain pine is common above 1300 feet. Samples 1 and 2, and phenological observations were taken on the knob. The Piedmont and the Blue Ridge, about 33 miles distant, are visible in the right background.

Several other known localities are not related to any major topographic feature. Such an area is in Hunterdon County, New Jersey, the easternmost record for the species. *Pinus pungens* has been there at least since the mid-1800's (Best, 1886), but probably it will remain in the area only if man-made disturbances are favorable for it. A stand of several hundred trees (partly planted, according to a local resident), being overtopped by hardwoods when visited in 1966, had almost no reproduction, although there were possible places for seedling establishment and growth near the stand. A limited number of *P. pungens* has been reported from just south of Newark, Delaware (for example, Tatnall, 1946). One small group of trees, again associated with human disturbance, was located during a short visit to the area in 1965. Similar areas have been reported, and at least one still exists, around Washington, D.C. (Ward, 1877; Kelley, 1931; and recent collections), and also in central Virginia (Kormanik & Little, n.d.) and central North Carolina (Coker & Totten, 1945, and recent collections). West of the main part of the range, specimens have been collected from Hawkins County, Tennessee; Summers County, West Virginia and from the Allegheny Plateau in Pocohantas and Randolph Counties, West Virginia (Allard & Leonard, 1952, and recent collections). Its northern limit corresponds

closely with the edge of the glaciated area in Pennsylvania. In this area, however, the pre-Wisconsin drift is scattered and topography shows no obvious influence of glaciation (Fenneman, 1938; Flint, 1957).

Within its range, Pinus pungens is unevenly distributed. It appears to be most abundant along the crest and eastern escarpment of the Blue Ridge, and in the shaly regions and on some of the higher ridges of the Valley-and-Ridge province. Between the Blue Ridge crest and the Valley-and-Ridge it appears to be rare, except in the south. Here it is quite common on the western slope of the mountains of the North Carolina-Tennessee border and some eastern Tennessee ridges, although not in the large region between the Great Smoky Mountains and the Blue Ridge crest.

Previous range maps of Pinus pungens are somewhat different from Fig. 2. Sudworth (1913) shows a much larger range than the present map. However, some reports on which he may have based his map have not been substantiated. Garman (1913) records a previous report for four counties in Kentucky, but no specimens or more recent reports have been found and the species apparently does not occur in Kentucky (Dr. E. T. Browne, personal communication). Harper (1901) based his report from northwestern Georgia on a misidentification (Harper, 1967). Mirov (1967) has

apparently copied Sudworth's map.

The range map in Critchfield & Little (1966) differs from Fig. 2 in one major way. Several personal collections and observations, examination of herbarium specimens, and conversations with U. S. Forest Service personnel have caused the inclusion of five counties in northeastern Georgia and areas of western North and South Carolina in which Critchfield & Little show a single location.

Pinus pungens has been planted at least in Bledsoe County, Tennessee (C. I. Peterson, personal communication) and Bedford and Cambria Counties, Pennsylvania (O. L. Mullhollen, personal communication), but such areas are omitted from Fig. 2.

Altitudinal Range

Pinus pungens occupies a rather wide altitudinal range. During this study collections were made from about 150 feet (46 m) near Newark, Delaware, to over 4700 feet (1430 m) in the Unaka Mountains, Unicoi County, Tennessee. In the Great Smoky Mountains of Tennessee and North Carolina, Stupka (1964) reports *P. pungens* from elevations up to 5800 feet (1767 m).

Of 89 areas where specimens were collected during this study, about 85 percent were at elevations between 1000 and 4000 feet (305 to 1220 m), with 10 percent below and 5 percent above. The 2000 to 3000 foot (610 to 915 m) interval includes more than the other thousand-foot intervals (31 percent).

Field Sampling Methods

Table Mountain pine stands were sampled in June and July, 1965, and from late May to early September, 1966. The locations of the samples are shown in Fig. 4. Characteristics of the sampling areas are listed in Tables 1 and 2.

1965 samples. These samples were intended to give information about the distribution and characteristics of *Pinus pungens* stands on which to base further sampling and experimental studies. Any stand with several trees of *P. pungens*, and not in the vicinity of a previous sample, was acceptable, regardless of its history. The 29 areas sampled included one roadbank stand and several stands obviously on old fields.

Figure 4. Location of sampling areas. Those sampled in 1965 are designated by numbers; those in 1966, by letters.

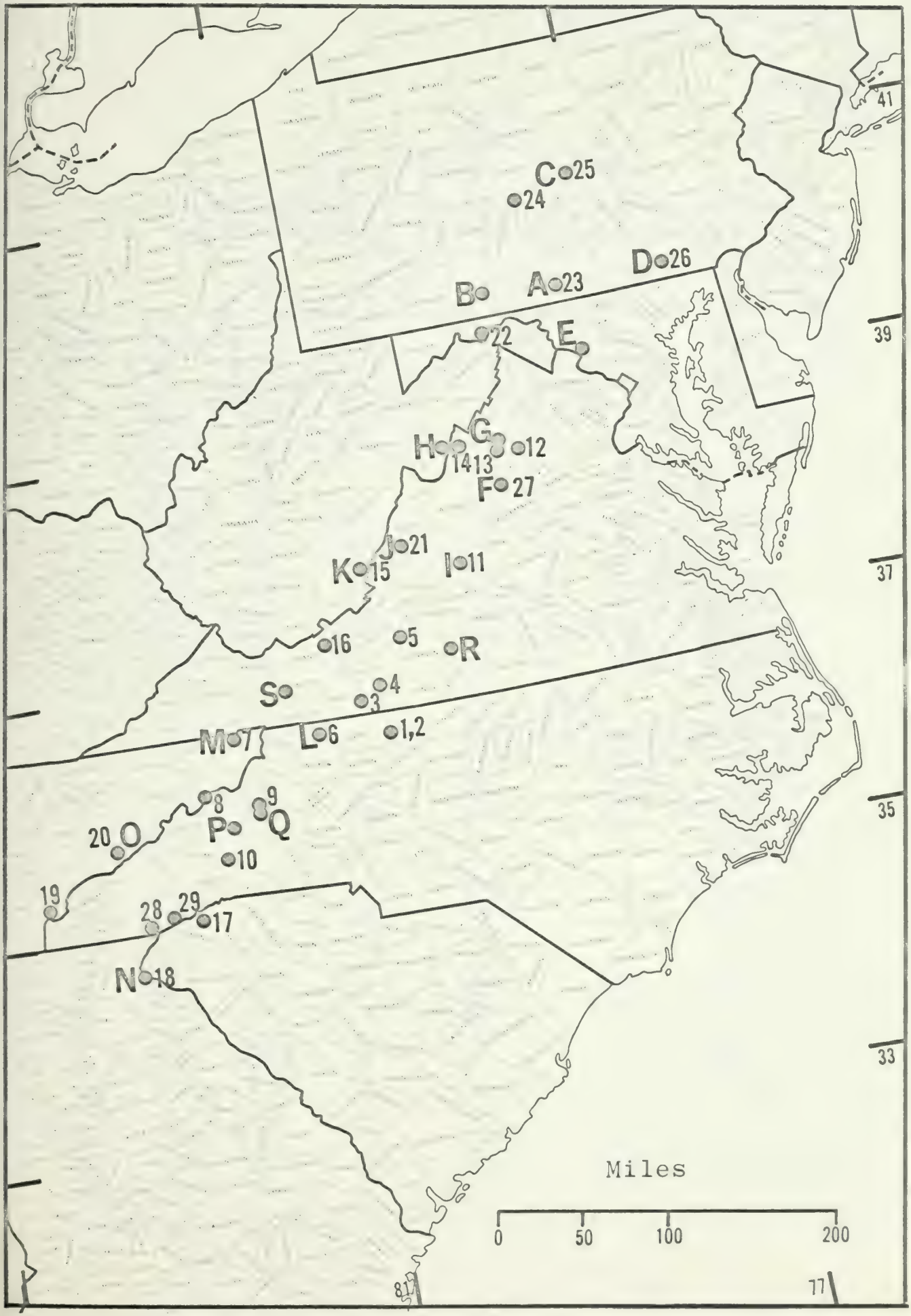

41
39
37
35
33
81
77
C 25
24
D 26
B
A 23
22
E
G
H
12
14 13
F 27
J 21
K 15
I 11
16
5
R
S
4
3
M 7
L 6
1,2
8
9
20
O
P
Q
10
19
28
29
17
N 18
Miles
0
50
100
200

Table 1

Characteristics at the centers of 1965 sampling areas. In "substrate" column, N = non-shale and S = shale.

Sample Area	Elevation (ft)	(m)	Slope (degrees)	Aspect (degrees)	Sub-strate	Topographic Position
1	2415	737	6	145-325	N	Ridgetop
2	1820	555	14	115	N	Slope
3	2850	869	4	---	N	Roadside, Flat
4	3220	982	10	5	N	Slope
5	2300	702	20	315	N	Slope
6	3560	1086	29	330	N	Rocky Bluff
7	2530	772	20	210	N	Slope
8	2770	845	30	150	N	Top of Lead
9	3540	1080	13	90	N	Slope
10	3100	946	18	220	N	Slope
11	1550	473	20	220	N	Slope
12	3640	1110	0	---	N	Ridgetop (Old Pasture)
13	1800	549	21	225	N	Rocky out-cropping
14	3350	1022	11	265	N	Ridgetop
15	2500	763	29	270	S	Slope
16	2580	787	5	---	N	Gentle Slope above Creek
17	2600	793	27	220	N	Rocky ridge
18	1300	397	16	245	N	Slope
19	2980	909	14	275	N	Slope
20	2950	900	11	145	N	Ridgetop
21	1600	488	17	175	S	Ridgetop
22	1340	409	5	250	N	Ridgetop
23	1475	450	21	290	N	Slope
24	950	290	6	---	N	Flat Old Field
25	1700	519	9	265	N	Ridgetop
26	400	122	36	220	N	Bluff
27	2900	885	27	260	N	Slope
28	4250	1296	0	---	N	Top of Knob
29	2800	854	0	---	N	Ridgetop

Table 2

Characteristics at the center of each subsample stand of 1966 sampling areas. In "substrate" column, N = non-shale and S = shale.

Sample Area	Pine or Oak	Elevation (ft)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Sub-strate	Total Basal Area (ft^2)	*Pinus Pungens* Basal Area (% of Total)	Topographic Position
A	Pine	1480	451	20	265	N	67	77	Slope
	Pine	1475	450	20	265	N	67	77	Slope
	Oak	1520	464	10	265	N	102	0	Slope
	Oak	1400	427	21	270	N	77	0	Slope
B	Pine	1250	381	13	280	S	82	27	Slope
	Pine	1260	384	17	290	S	67	21	Slope
	Oak	1280	390	17	260	S	72	0	Shallow Gully
	Oak	1240	378	17	260	S	72	0	Shallow Gully
C	Pine	1100	336	6	130	N	108	43	Old Field
	Pine	960	293	29	207	S	75	59	Bluff
	Oak	1145	349	8	145	N	65	3	Slope
	Oak	1070	326	32	110	S	76	3	Bluff
D	Pine	375	114	27	218	N	37	23	Bluff
	Pine	375	114	27	218	N	37	23	Bluff
	Oak	400	122	21	122	N	58	0	Slope
	Oak	275	84	35	193	N	51	0	Bluff
E	Pine	1100	336	28	170	N	67	59	Slope
	Pine	1200	366	24	280	N	55	31	Rocky Point
	Oak	1035	316	18	175	N	64	0	Slope
	Oak	1200	366	19	190	N	70	0	Slope

Table 2 (continued)

Sample Area	Pine or Oak	Elevation (ft)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Sub-strate	Total Basal Area (ft^2)	*Pinus pungens* Basal Area (% of Total)	Topographic Position
F	Pine	2960	903	25	242	N	38	55	Talus slope
	Pine	2920	891	25	242	N	38	55	Talus slope
	Oak	2955	901	27	205	N	45	15	Talus slope
	Oak	2985	910	25	105	N	80	0	Slope
G	Pine	1535	468	18	235	N	73	42	Rocky Sloping Ridgetop
	Pine	1490	454	26	227	N	47	60	Rocky Sloping Ridgetop
	Oak	1550	473	26	160	N	50	3	Slope
	Oak	1455	441	26	230	N	64	0	Slope above Creek
H	Pine	1990	607	21	270	S	67	44	Ridgetop
	Pine	1960	598	18	240	S	67	23	Ridgetop
	Oak	2005	612	24	340	S	81	0	Bluff
	Oak	1970	601	37	65	S	96	0	Slope
I	Pine	1700	519	15	237	N	94	82	Slope
	Pine	1690	515	25	220	N	72	48	Slope
	Oak	1770	540	20	145	N	87	2	Slope
	Oak	1700	519	20	130	N	66	4	Slope
J	Pine	1610	491	11	225	S	60	66	Ridgetop
	Pine	1595	486	19	265	S	67	49	Slope
	Oak	1570	479	33	115	S	37	7	Slope
	Oak	1580	482	12	260	S	62	4	Bench above Creek
K	Pine	2605	795	26	260	S	48	61	Slope
	Pine	2640	805	29	250	S	70	71	Slope
	Oak	2600	793	31	275	S	49	5	Slope
	Oak	2480	756	30	250	S	75	0	Slope

Table 2 (continued)

Sample Area	Pine or Oak	Elevation (ft)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Sub-strate	Total Basal Area (ft^2)	*Pinus pungens* Basal Area (% of Total)	Topographic Position
L	Pine	3600	1098	26	260	N	66	74	Top of Bluff
	Pine	3540	1080	29	250	N	41	83	Bluff
	Oak	3550	1083	31	275	N	51	5	Deep Gulley
	Oak	3540	1080	30	250	N	88	0	Gulley
M	Pine	2510	766	26	235	N	56	66	Slope
	Pine	2480	756	22	240	N	72	71	Slope
	Oak	2455	749	27	275	N	71	4	Slope
	Oak	2415	737	38	200	N	68	0	Slope
N	Pine	1290	393	15	240	N	67	72	Slope
	Pine	1210	369	28	267	N	60	91	Bluff
	Oak	1330	406	13	35	N	58	0	Slope
	Oak	1170	357	37	255	N	56	8	Bluff
O	Pine	2355	718	23	187	N	73	56	Slope
	Pine	2315	706	35	217	N	83	24	Slope
	Oak	2360	720	37	245	N	85	24	Slope
	Oak	2300	702	34	275	N	68	4	Slope
P	Pine	4620	1409	27	135	N	85	100	Lead
	Pine	4610	1406	31	152	N	57	94	Lead
	Oak	4610	1406	34	88	N	57	0	Slope
	Oak	4600	1403	42	358	N	--*	0	Bluff
Q	Pine	3580	1092	23	225	N	54	78	Rocky Point
	Pine	3605	1100	6	257	N	54	50	Top of Rocky Bluff
	Oak	3625	1106	21	115	N	61	4	Ridgetop
	Oak	3620	1104	28	245	N	106+	5	Ridgetop

* shrub heath

\+ almost pure *Pinus rigida*

Table 2 (continued)

Sample Area	Pine or Oak	Elevation (ft)	Elevation (m)	Slope (degrees)	Aspect (degrees)	Sub-strate	Total Basal Area (ft^2)	*Pinus pungens* Basal Area (% of Total)	Topographic Position
R	Pine	1580	482	18	185	N	78	16	Slope
	Pine	1560	476	15	177	N	76	19	Slope
	Oak	1590	485	10	115	N	74	0	Ridgetop
	Oak	1490	454	19	72	N	56	0	Slope
S	Pine	2585	788	28	255	S	71	56	Slope
	Pine	2600	793	32	250	S	58	53	Slope
	Oak	2565	782	42	235	S	58	3	Slope
	Oak	2560	781	44	30	S	49	9	Bluff

For each sampling area the following information was recorded: topographic position, aspect, slope, elevation, rock outcrop as an estimated percent of the area, drainage ("excellent", "poor", etc.), litter cover ("thick", "thin and spotty", etc.), and comments regarding stand disturbance, cone serotiny, cutting of cones by squirrels, and other general characteristics of the stand. Rock and soil were sampled and depth of soil recorded. Three Table Mountain pines were sampled in each stand. Height, using an abney level and pacing; diameter, measured at 54 inches (1.37 m or DBH) with a diameter tape; and an increment core were taken. Needles, a herbarium specimen and cones were collected where they could be reached with a tree trimmer mounted on a telescoping twenty-foot pole. Comments about the form and vigor of each tree were also recorded.

Species lists for the canopy stratum, the understory-and-shrub stratum and the ground-cover stratum were compiled. Each species was assigned a number indicating its importance within each stratum ("importance rating"). This scale, based on one used by Oosting (1948) and similar to that used by Rodgers (1965) was:

1 = Infrequent in the sample area.

2 = Scattered more or less throughout the area.

3 = Frequent, but not dominant, or, in the lower strata, dominant in a few small clumps.

4 = Locally dominant within the area.

5 = Dominant over extensive portions of the sample area.

Voucher specimens collected for identification and documentation of vegetation data during both 1965 and 1966 are in the herbarium of Duke University. Nomenclature follows Fernald (1950) except where noted by inclusion of authority.

1966 samples. Sampling in 1966 was designed to determine differences between habitats supporting *Pinus pungens* and those adjacent habitats where the species was absent or only a minor part of the vegetation. Nineteen areas, designated by letters on Fig. 4, were sampled. Eleven of the 1965 areas were resampled; eight samples were in new areas. Criteria for selection of stands were more exclusive than in 1965. Stands with minimum obvious recent disturbance, and having naturally determined boundaries, were chosen. Twenty Table Mountain pines were included in the sample at each area, setting a lower limit on stand size. These

criteria excluded several of the stands sampled in 1965. As in 1965, samples chosen represented all portions of the range of P. pungens.

At each sample area, four subsample "stands" were located, two being "Table Mountain pine" and two "oak". The Table Mountain pine stands were chosen from the part of the sample area where it had its maximum importance; the "oak" stands were chosen from areas adjacent to pine stands, where P. pungens was absent or infrequent. Stands were chosen to represent the variation in topographic position at the sample area. For example, in a stand of Pinus pungens on the top and one side of a ridge, one "stand" would be chosen from the ridgetop, another from the slope. The oak stands could be below the pine, or over the ridge from it, or around the slope on the contour. Where stand size was small, the pine stand samples were sometimes taken in distinct neighboring stands.

The elevation, slope, aspect, drainage, and a subjective measure of ground and shrub cover at the center of each subsample stand were recorded. Two "Sixes" maximum-minimum thermometers with aluminum shields were attached to a tree in each stand. Sensing elements were placed about 54 inches and 6 inches (137 and 15.4 cm) from the ground, on the north side of the tree. Thermometers were left in place

during the two to four days spent collecting in each area, and temperatures were recorded each day. At some sample areas, relative humidities were determined at the center of each stand, with a cog psychrometer.

Near the center of each stand, top- and subsoils were sampled and depths of litter and topsoil recorded. "Topsoil" was defined as the horizon obviously showing the effects of incorporated organic matter. Soil temperatures were taken under the litter layer and at 2, 10, 20, and 40 cm deep in the mineral soil at each soil collection point. Except immediately after rains, samples for soil moisture determinations were taken in each stand, at the soil collection point, and placed in aluminum boxes with tight lids. Rock outcrop, as an estimated percent of the area, was recorded and a rock sample taken from each stand.

In each Table Mountain pine stand, ten individuals of *Pinus pungens* were sampled, and height, DBH, length of live crown and of clear bole as an estimated percent of total height, and a vigor notation were recorded. Increment borings, and needles and cones, where they could be reached, were collected. Herbarium specimens were collected from two to five trees per area. One specimen from each area has been deposited in the Duke University herbarium. In oak stands, diameters and species of ten trees, and heights and ages of

dominants were determined. Vegetation in each stand was recorded as in 1965, except that tree saplings, tree seedlings, and shrubs were recorded separately. Other facts about the stand (evidence of fire, cone-cutting by squirrels, etc.) were recorded.

The basal area of each stand was estimated by the variable-radius method of Bitterlich (Phillips, 1959), using a wedge prism as the angle gauge. One point was at the center of the stand and, where the points would sample the intended stand, others were at a distance of 66 feet upslope, downslope, and in both directions along the contour. Total basal area and basal area of Table Mountain pine were estimated from the numbers of trees counted.

Treatment of soil samples. Percent moisture in soil samples was determined gravimetrically, both for the total sample and corrected for the stones in the sample (Reinhart, 1961). Part of each soil sample was sent to the Soil Testing Division of the North Carolina Department of Agriculture for chemical analysis. Soil pH, percent organic matter, and concentrations of "available" phosphorus, calcium, magnesium, potassium, manganese, nitrate and ammonium were determined from $HCl-H_2SO_4$ extracts by methods outlined in Reid & Copeland (1966). Cation exchange capacity and exchangeable aluminum were determined for a few sample areas.

Soil texture was determined for sample areas C, D, G, H, J, N, P, Q, and S by the hydrometer method (Bouyoucos, 1936). Using a ceramic plate apparatus (L. A. Richards, 1965) the water contents of all soils were determined at 15 atmospheres and at 1/3 atmosphere of tension. The "water holding capacity" of each soil was calculated by subtracting the water content at 15 atmospheres from that at 1/3 atmosphere.

Factors Associated with *Pinus pungens*

Topographic position. Stands of *Pinus pungens* are usually associated with exposed sites where drainage is extremely rapid, soil is often very shallow and rock outcrop may be extensive. Areas of rock outcrop are rather rare in the Appalachian Mountains and are more likely to be associated with recent stream-cutting than with divides and summits (Fenneman, 1938). The influence of such topography on the occurrence and characteristics of vegetation was emphasized by Racine (1966). Well-developed pine stands of the southern Blue Ridge Escarpment occur only in specific topographic situations, with best development on narrow ridges, well exposed to the south or west. Several Table

Mountain pine stands sampled in this study were in such topographic situations, all along the Blue Ridge or outlying mountains (samples E, F, G, L, P and Q), and others have been described in the literature (for example, Nuttall, 1857; Allard & Leonard, 1943).

Table Mountain pine also occurs on exposed mountain slopes, usually fairly steep ones. In Pennsylvania, stands found were almost exclusively associated with steep slopes rather than with ridgetops and leads. Steep lower and middle slopes frequently support stands in the Ridge-and-Valley province, where the species is often associated with shale outcroppings at relatively low elevations. Allard (1946) and Illick (1928) record the association of Pinus pungens with shale embankments, and samples B, C, H, J, K and S have further examples of it (See Fig. 5). In the Valley-and-Ridge province the species is also found on ridge-capping sandstones at higher elevations (samples 14, M) or on lower non-shale outcroppings (samples 13, G). Sample N, occupying an exposed sandy bluff between a clay upland and a creek bottom, is unique among the areas seen during this study.

Pinus pungens grows in other topographic situations, even in moist areas at the base of mountains (Illick, 1928), as found in one stand of sample C and in sample 16. However, such stands observed in this study appeared to be on disturbed

Figure 5. An open Table Mountain pine stand on a steep shale slope at area C, Bald Eagle State Forest, Snyder County, Pennsylvania, at 960 feet elevation. Many age classes are present, from year-old seedlings to trees with almost 200 rings. There is evidence of repeated fires.

areas and none were effectively reproducing. Specimens have also been collected from around bogs on Mt. Pisgah, North Carolina, and at Big Meadows, Shenandoah National Park, Virginia.

Aspect. Not all sharp, rocky ridges or steep, rocky slopes are equally likely to support stands of *Pinus pungens*. The aspect (direction the slope faces) has a large effect in determining if *Pinus pungens* will be present, as noted by Cain (1931), Whittaker (1956), and Stupka (1964) for the Great Smoky Mountains, by Racine (1966) for the Blue Ridge and Hack and Goodlett (1960) in western Virginia. This situation prevails throughout the range of the species. On Fig. 6, a contour map of a hypothetical conical mountain, the elevation and aspect of stand centers of samples shown on Fig. 4 are plotted. Each point represents the center of one or two of 47 stands. All 1966 stands, and 1965 stands not resampled in 1966, are plotted except those with a slope less than 15 percent (about 9 degrees). For areas with little slope, aspect makes a minimal difference and is difficult to determine. Subsamples of 1966 areas are plotted separately if they were separated by more than 50 feet of elevation or 10 degrees in aspect. There are 34 stand centers in the southwest quadrant, 6 in the southeast, 5 in the northwest and 2 in the northeast. The one stand with a

Figure 6. A contour map of a hypothetical conical 5000-foot mountain, showing the elevation and aspect at the center of 47 Table Mountain pine stands. Large dots represent centers of two stands. Stands with slope of less than 15% were not plotted.

north aspect is on an old field with an 18 percent slope, and contributes little to dispute the contention that the species usually occurs on southwest-facing slopes. From Fig. 6, higher elevation stands appear less limited to the southwest aspect than those at lower elevations.

Exceptions to the general rule should be noted, however. On Rocky Face, a small monadnock in Alexander County, North Carolina (Keever et al., 1951), the pine occurs only on a north slope about 1800 feet (549 m) in elevation, although apparently similar areas are available on other aspects on the mountain. It is limited to a north and northwest facing bluff along the Pigg River in Virginia.

Aspect, alone, can have no effect on tree distribution. However, it profoundly influences the climate of a slope (Billings, 1952; Geiger, 1965). The direct beam irradiation on slopes is greatly influenced by aspect. "Potential solar beam irradiation" is irradiation the slope would receive if atmospheric turbidity were absent, and can be considered as a slope parameter, changing only in the annual cycle. Compiled from tables of this parameter in Frank & Lee (1966), Table 3 illustrates the influence of aspect at 38 degrees N latitude, for a 40 percent slope. (The average slope for the 38 pine stands sampled in 1966 is 42 percent or 23 degrees.) Differences between aspects are greatest in the winter.

Table 3

Daily potential solar beam irradiation in Langleys at 38°N for a 40 percent slope (from Frank and Lee, 1966).

Aspect	June 22	Date March 21 Sept. 23	Dec. 22
North	971.5	461.3	51.3
NE, NW	969.0	549.1	159.9
E, W	986.0	711.7	366.0
SE, SW	969.3	836.6	563.8
South	942.9	880.7	655.7

Sky radiation, resulting from atmospheric turbidity, is essentially equal for all aspects and tends to equalize the radiation received, although measurements of total radiation still show large differences with aspect (Geiger, 1965).

Wind and moisture conditions also affect the climate of different aspects. There may be local precipitation differences on different aspects. Soil and air temperature also change with aspect. The southwest slope can be expected to be the warmest, because it receives its maximum radiation during the afternoon when most of the energy is used to heat the soil and the air. Research cited by Geiger (1965) shows the warmest area on a somewhat conical mountain to be in the middle of the southwest slope, and the coldest in the middle of the northeast slope. Evaporation

measurements followed the same pattern. Parker (1952) used similar microclimatic patterns, integrated as differences in soil moisture, to account for species distributions in northern Idaho.

Within the range of Pinus pungens (near sample area 29) a recent two year study of environmental, vegetational, and phenological gradients on opposing north and south slopes further illustrates the effect of aspect on microclimate and species distribution (Mowbray, 1967). The following factors increased from lower to upper slopes and from the north- to the south-facing slope: annual insolation, air and soil temperatures, vapor pressure deficit, and evaporation. Differences in soils were also found. Clay content increases, sand content decreases, and clay type changes from the north to south slopes, and upslope. Upper slopes have a greater water storage capacity than lower ones, although soil depth increases downslope. Mowbray concludes that the most important factor controlling species distribution in this area, which has an annual rainfall of 90-100 inches (229-254 cm) is not soil moisture but rates of evapotranspiration. Although the rainfall is much above that found throughout most of the range of Pinus pungens, this area probably shows many features which would appear in comparisons of north and south slopes elsewhere within the range of the species.

Losche (1967), working a few miles south of sample S in Smyth County, Virginia, found that mean annual soil temperature on a south slope at 50 cm was 2 C higher than on the north slope. The maximum difference of 5 C occurred in the winter.

From Fig. 6 and the aspect-microclimate relationships discussed above, it appears that Pinus pungens occurs most often on areas with the warmest and driest microclimate available.

A detailed study of the relationships of geomorphology and vegetation was made about 15 to 20 miles SSW of area 14, in western Virginia (Hack & Goodlett, 1960). Vegetational distributions were interpreted in terms of soil moisture conditions. Pinus pungens is an important member of the "yellow pine forest", which occupies only those areas which are convex away from the mountain, the "noses", and ridges. These areas theoretically receive minimal runoff water and seepage from slopes above, while concave areas receive the maximal amount. Effects of topographic position, soil mantle texture, dip and nature of geologic strata, exposure, altitude, and assymetry of opposing slopes also influence the moisture regime. This study indicates that many factors besides microclimate, considered primary in the previous discussions, may influence moisture conditions and therefore

influence species distribution. Such factors may explain presence or absence of Pinus pungens in situations which contradict the general relationships found in the present study.

Microtopographic distribution. Even within Table Mountain pine stands, fairly consistent differences in species distributions occur. While Pinus pungens and P. virginiana usually occur throughout the site, P. rigida sometimes is restricted to areas on the periphery of the stand. It may be on the lower part of a shale slope, but not the top of the ridge, or to the side of a rocky outcrop, while the other pines grow on the most extreme parts of the substrate as well.

In some cases, especially at areas D and L, pines and oaks are generally segregated within the pine stand. The bedrock appears to be in laterally overlapping layers, like a shingled roof tipped sideways. P. pungens occurs on the thin soil on the exposed rock outcropping, while oaks are in the "trough" between the end of one "shingle" and the base of the next, where more soil has accumulated and where water probably accumulates. At area Q, Table Mountain pine is on the end and around the edges of a rocky point, but the center is dominated by pitch pine.

In many cases, P. pungens is strictly limited to the southwestern aspects. Other pine species may occur further

"around the hill", or over the top of the ridge. In some shale areas, P. virginiana is much more common than the other pines on the open eastern or northern slopes.

Geology. Meehan (1889) noted that Pinus pungens in Pennsylvania was then known to grow only on upper Silurian and perhaps lower Devonian rocks. This suggestion of a substrate specificity of the species was followed up in the present study by correlating its occurrence with the geological formation on which it was found. Any preference for certain substrates might suggest what factors limited the range. Using the most recent geological maps that could be found, the formation upon which the species grew was determined for 68 observations. In borderline cases, samples of rock from the sites were compared to descriptions given for the strata involved. Table Mountain pine occurred on 20 named formations and 3 groups of unnamed strata. Six of the named formations, plus unnamed gneisses and schists, account for 48 of the 68 locations. These formations are listed in Table 4.

Which formations are equivalent is difficult to determine, but the situation presented in the table is the best summary that could be extracted from the references listed.

Table 4

Geological formations on which Pinus pungens was observed three or more times. (Geological information from Allen, 1963; Brent, 1960; Bryant, 1962; Hadley and Goldsmith, 1963; Keith, 1894; King and Ferguson, 1960; Knopf and Jonas, 1929; Legrand, 1960; Nelson, 1962; N. C. Dep. Conservation and Development, 1958; Penn. Dep. Internal Affairs, 1960; Price and Heck, 1939; Reed, 1964; Tilton et al., 1927; U. S. Dep. Interior, Geol. Surv.; Virginia Div. Mineral Resources, 1963; Vokes, 1957).

Formation	Age	No. Locations	Geographic Area
Wilson Creek Gneiss	p€	4	Blue Ridge, Burke Co.,N.C.
Snowbird Fm.	p€	3	Valley-and-Ridge Province, Tenn.
Chilhowee Gp. (Unicoi, Loudon, Weverton, Erwin Fm)	€	9	Blue Ridge and outliers, Northern Va. and Md.; northeast Tenn. and southwest Va.
Hampton, Harpers Fm.	€	3	Northeast Tenn., southern Penn., central Va.
Clinton, Tuscorora Fm.	S	4	Massanutten Mtn., Va.; central Penn.
Chemung, Portage Fm., includes Brallier Shale	D	8	Valley-and-Ridge, southwestern Va. to southern Penn.
Hampshire, Catskill Fm.	D	7	Valley-and-Ridge, central Va. and W. Va.
Unnamed Gneisses & Schists	?	10	Piedmont monadnocks and Blue Ridge, southern Va. to Md.

It appears that Pinus pungens is associated to some extent with certain geologic strata. Part of this association is due to the type of topographic forms the strata take under weathering, such as the shaly ridges and embankments found on the Chemung-Portage formation, and the sharp ridge outcrops of the Chilhowee group. Part of the association of the pine with these formations may also be due to chemical and physical characteristics related to soil formation and to supporting plant growth.

Pinus pungens was not found on limestone. The only record of its occurrence on limestone is a herbarium specimen (NCU) collected near Linville Caverns, McDowell County, North Carolina.

Soils. Occurrence of Pinus pungens on different soil series shows a pattern similar to that with geology. The soil series for 38 separate occurrences of the pine were determined from the appropriate Soil Surveys of the U. S. Department of Agriculture. Eleven soil series and the general category of "rough stony land" were associated with Pinus pungens. The most common series are listed in Table 5. Soils classified as "rough stony land" with soil material of a given series are listed under the series name.

Table 5

Soil series on which *Pinus pungens* was observed in four or more places. (Data from U. S. Dep. Agr., Soil Surveys.)

Series	No. Locations	Region
Ashe	4	N.C. Blue Ridge
Dekalb	5	Valley-and-Ridge, W. Va. to southern Penn.
Porters	5	Blue Ridge, S.C. to central Va.; South Mountains, N.C.
Ramsey	5	Eastern Tenn. and southwestern Va.
Ashe-Porters-Ramsey	1	Grandfather Mountain, N.C.
"Rough stony land" (no series listed)	5	Blue Ridge and eastern outliers

The soil series where Table Mountain pine is found are generally stony; shallow, sometimes without profile development; strongly acid; infertile and of low productivity; and well to excessively drained (U. S. Dep. Agr., Soil Surveys). The species usually occurs where soil development is minimal, so the conditions listed above are expressed in their extreme form on areas where it grows.

The soil series have somewhat the same pattern as the geologic strata. Four of five Dekalb soils are on Chemung-

Portage Formation rocks, for example.

The soils sampled during this study contained large numbers of loose rocks, up to a foot or more in size. In some cases the only "soil" was a mat of organic matter and roots between or over the rock. After all stones over about an inch diameter were discarded, soil samples still contained large amounts of gravel (Table 6).

Table 6

Gravel over 2 mm. diameter in soil samples.
Percent of air-dry weight.

Horizon	Non-shale Areas (27 stands)		Shale Areas (11 stands)	
	Pine	Oak	Pine	Oak
Topsoil	31	30	54	56
Subsoil	38	38	59	59

Physical and chemical characteristics of the 1966 sample area soils for Table Mountain pine and oak stands are summarized in Table 7. All values are averages for 38 stands except texture and aluminum (16 stands), and cation exchange capacity (6 stands). Table Mountain pine stands have less sand, more clay, a lower pH and lower concentrations of mineral nutrients in both top and subsoils. Differences in concentrations of calcium, magnesium, and manganese are

Table 7

Average characteristics of soils from 1966 sample areas, (± one standard deviation). 1 lb/acre = .92 kg/ha.

Characteristic	No. Areas	Topsoils Pine	Topsoils Oak	Subsoils Pine	Subsoils Oak
Sand (percent)	8	61±10	63±10	49±11	53±11
Silt (percent)	8	28±8	27±8	30±9	28±7
Clay (percent)	8	11±5	11±6	21±11	18±8
Water holding capacity (%)	19	14±6	14±7	16±6	16±6
Depth (cm)	19	7.7±5.7	8.8±6.8		
Depth of litter (cm)	19	5.1±2.4	4.9±2.5		
Organic matter (percent)	19	5.5±2.2	6.0±2.3	2.5±1.5	2.4±1.5
pH	19	4.0±.3	4.2±.4	4.4±.2	4.5±.3
Ca (lb/acre)	19	107±83	275±314	45±37	84±93
Mg (lb/acre)	19	27±12	56±40	24±17	40±32
P (lb/acre)	19	5.2±3.3	7.3±5.6	6.8±10.8	7.5±9.2
K (lb/acre)	19	91±46	122±54	68±28	89±60
Mn (lb/acre)	19	36±105	138±182	21±34	56±89
NO_3 (ppm)	19	2.0±1.7	1.5±.8	1.5±.6	1.9±1.5
NH_4 (ppm)	19	19±15.0	17.5±10.2	19±15.0	17.5±10.2
Al (me/100 g)	8	12±4	13±4	4±3	4±2
* CEC (me/100 g)	3			11.5±3.8	9.5±5.4

* Cation Exchange Capacity

the largest. Variation between sample areas is great.

An "average" topsoil for a pine stand is a sandy loam; the subsoil is a loam. In oak stands, 13 had sandy loam topsoils; 8 had loam subsoils and 5 had sandy loam subsoils. Twelve oak stands had sandy loam topsoils; seven subsoils were sandy loams and six were loams.

The differences in soil characteristics found were not unexpected. Losche (1967) and Mowbray (1967) found similar differences between north and south slopes in the southern Blue Ridge escarpment, although Losche found fewer differences between slopes in southwestern Virginia, where the soil developed from quartzite. Although the pine-oak comparison made here is not strictly a north-south slope comparison, the differences in vegetation on the areas compared are somewhat the same. Which differences between stands are probably significant to the distribution of *Pinus pungens* will be discussed later, for those characteristics measured for most soils. Analysis of variance of exchangeable aluminum and cation exchange capacity data showed no differences between pine and oak.

The data in Table 7 represent the situation which would exist with all substrate particles less than 2 mm in diameter. In chemical analyses presented as lb/acre the

further condition of a "furrow-slice" depth for each horizon is assumed. Both assumptions cause overestimation of nutrient content and water holding capacity of the sites upon which Pinus pungens grows. The large amount of gravel (Table 6), larger stones which may occupy the majority of volume of the substrate, and bedrock under shallow soils greatly reduce the percent of the volume of substrate for which the soil analyses are valid. Since soils vary in depth and stoniness, and since the roots of Table Mountain pine may occupy cracks in the bedrock, there is no way to estimate accurately the supply of water and nutrients trees may have. However, because the physical conditions of the site reduce the volume of soil material, already low in nutrients, it appears that these sites have a small nutrient supply available. Accurate comparison of different sites would require information about actual soil volumes and rooting depths. However, the available information is a first approximation of the conditions existing on different sites.

Some chemical analyses are presented as lb/acre to avoid the assumption of a standard "volume weight" for all soil samples. Analyses on samples of measured volume make such an assumption or the determination of "volume weight" necessary to express nutrient concentration on a weight basis (P. H. Reid, personal communication). The use of these units

allows comparisons of soils with different densities by presenting the amount of nutrient in a standard volume of soil.

Vegetation. The vegetation on sites where Table Mountain pine occurs has relatively few species (Table 8).

Table 8

Average number of higher plant species per stand, 1966 sample areas.

Stand	Geological Substrate	Trees Over-story	Trees Under-story	Seedlings	Shrubs	Ground Cover	Total
Table Mountain Pine	Shale	5.3	7.5	8.9	6.4	6.4	23.8
	Nonshale	4.7	6.3	6.4	6.9	5.3	22.6
	Total	4.9	6.6	7.1	6.7	5.6	22.9
Oak	Shale	4.5	8.8	9.8	5.3	7.3	26.9
	Nonshale	4.4	6.0	6.3	5.9	5.4	20.9
	Total	4.4	6.8	7.3	5.7	5.9	22.6

The numbers in each row do not add to the "total" because a given tree species may occur in one to three different columns.

The data in Table 8 show that, on the average, Table Mountain pine stands had about the same number of species as the neighboring stands without the pine. However, on a given

substrate there was a marked difference, pine having more than oak off shale, but fewer on shale. The main differences between pine and oak, on the average, were in the shrub stratum and the overstory, where pine stands had 1.0 and 0.5 more species, respectively. A greater difference existed between stands on shale and those not on shale, especially in oak stands. Stands on shale had more species in all tree strata and in the ground cover, and fewer shrub species. The greater number of ground cover species and seedlings was probably related to the lower shrub cover, since the relative reduction in shrub cover observed on most shale stands was greater than the reduction in shrub species number. Soil surface of many shale stands is partly covered by fruticose lichens.

Because most stands were visited only once, the number of herbaceous ground-cover species reported could be lower than it should be, due to missed early- or late-season plants. However, these appear to be insignificant except in a few areas and the numbers of species given in Table 8 should reflect the true situation.

Tables 9 and 10 show the percent presence, and average importance rating when present, of all species which occurred in four or more pine or oak stands of the 38 sampled in 1966.

Table 9

Percent presence of tree species in 38 Table Mountain pine and 38 oak stands, 1966 sample areas. (Average importance rating when present shown in parentheses.)

	Species	Overstory		Understory		Seedlings	
		Pine	Oak	Pine	Oak	Pine	Oak
TREES	Pinus pungens	100(4.5)	26(1.1)	82(2.1)	11(1.5)	68(1.7)	11(1.5)
	Quercus prinus	76(2.6)	95(4.3)	71(1.8)	74(2.1)	55(1.8)	87(2.0)
	Q. coccinea	71(2.0)	53(2.7)	42(2.0)	26(1.8)	45(1.4)	26(1.6)
	P. rigida	66(2.9)	29(3.0)	47(1.6)	26(1.5)	29(1.5)	11(1.3)
	P. virginiana	53(2.0)	13(2.2)	47(2.0)	21(1.8)	37(1.7)	29(1.3)
	Q. velutina	24(1.1)	26(1.4)	26(1.3)	18(1.4)	29(1.5)	18(1.6)
	Betula lenta	16(2.5)	18(1.1)	26(2.0)	16(1.7)	11(1.8)	16(1.5)
	P. strobus	16(1.0)	13(1.2)	37(1.1)	16(1.8)	26(1.3)	26(1.4)
	Acer rubrum	13(1.2)	29(1.5)	37(1.7)	61(2.3)	50(1.5)	58(2.0)
	Q. rubra	11(1.5)	45(2.6)	11(1.3)	18(1.7)	5(1.5)	39(1.5)
	Q. alba	11(1.0)	11(2.3)	16(1.7)	18(1.3)	26(1.0)	16(1.3)
	Nyssa sylvatica	--	--	58(2.3)	55(2.3)	50(1.9)	39(1.7)
	Amelanchier spp.	5(1.0)	--	37(1.7)	26(1.3)	42(1.4)	29(1.1)
	Q. marilandica	8(1.7)	8(3.3)	26(2.5)	18(2.1)	21(1.8)	13(1.3)
	Sassafras albidum	5(1.0)	--	26(2.4)	29(1.3)	79(1.7)	74(1.6)
	Oxydendrum arboreum	8(1.0)	11(2.0)	21(2.4)	24(2.6)	11(1.8)	3(2.0)
	Carya spp.	3(1.0)	34(1.9)	13(1.0)	58(1.6)	32(1.2)	55(1.6)
	Robinia pseudo-acacia	--	13(1.8)	11(1.0)	16(1.3)	34(1.3)	39(1.3)
	Cornus florida	--	--	8(1.7)	39(2.2)	11(1.5)	26(2.1)
	Tsuga canadensis	3(1.0)	5(1.0)	3(5.0)	5(3.0)	8(1.3)	24(1.2)
	Acer pensylvanicum	--	--	--	5(1.0)	--	11(1.0)

Table 10

Percent presence of shrub and ground-cover species in 38 Table Mountain pine and 38 oak stands, 1966 sample areas. (Average importance rating when present shown in parentheses.)

		Pine	Oak
SHRUBS	Kalmia latifolia	84(3.3)	87(2.5)
	Vaccinium vacillans (+ V. pallidum)	82(2.9)	63(2.6)
	Smilax spp.	74(2.0)	47(1.8)
	Gaylussacia baccata	71(4.0)	37(2.6)
	V. stamineum	66(1.9)	63(1.9)
	Castanea dentata	55(1.9)	63(1.8)
	V. angustifolium	45(2.2)	32(1.6)
	Q. ilicifolia	39(2.9)	11(2.0)
	Hamamelis virginiana	24(1.4)	45(2.2)
	Rhododendron catawbiense	18(2.9)	16(1.8)
	Leucothoe recurva	18(2.1)	8(2.7)
	Viburnum acerifolium	18(1.6)	26(1.5)
	R. minus Michx.	11(3.3)	11(2.8)
	Hypericum sp.	11(2.5)	3(1.0)
	R. maximum	5(1.5)	14(2.4)
	Vitis spp.	5(1.0)	29(2.0)
GROUND COVER	Pteridium aquilinum	53(1.9)	32(1.3)
	Tephrosia virginiana	37(2.4)	----
	Epigaea repens	37(1.5)	16(1.7)
	Gaultheria procumbens	34(1.8)	32(2.0)
	Galax aphylla	24(2.4)	24(2.3)
	Panicum spp.	18(1.0)	24(1.4)
	Iris sp.	13(2.0)	13(1.2)
	Polystichum acrostichoides	11(1.8)	16(1.0)
	Baptisia tinctoria	11(1.3)	----
	Chimaphila maculata	11(1.0)	13(1.2)
	Potentilla spp.	11(2.0)	21(1.1)
	Uvularia spp.	8(1.0)	11(1.3)
	Dioscorea villosa	5(1.5)	34(1.5)
	Aralia nudicaulis	5(1.0)	11(2.0)
	Hieraceum sp.	5(1.5)	13(1.2)
	Dryopteris spp.	3(1.0)	16(1.2)
	Parthenocissus quinquefolia	3(1.0)	16(1.7)

Table 10 (continued)

	Pine	Oak
Asplenium platyneuron	----	18(1.2)
Mosses on soil	55(1.3)	66(1.9)
Lichens on soil	24(3.0)	24(1.9)

Some problems of species identification should be mentioned here. Field identifications of Vaccinium species used in statistical analyses presented below were not always confirmed by later work with specimens. V. vacillans and V. pallidum are lumped in these analyses as V. vacillans. Specimens tentatively identified as these two species or as V. angustifolium showed continuous range of variation in some key characters, making identifications approximate at best. Specimens best fitting descriptions of V. angustifolium or varieties (Fernald, 1950) were collected well south of its reported range (Reiners, 1965). Results utilizing these identifications must be interpreted cautiously.

Table Mountain pine stands have few important species present throughout the range. Several of the more important species which occur with the pine are restricted to one end of its range. Quercus ilicifolia, Viburnum acerifolium and Vaccinium angustifolium are most important in the northern part of the range and absent from the extreme southern part; the evergreen Rhododendrons, Epigaea repens and Galax aphylla are important only south of Virginia. Among tree species, Q. velutina is important only in the north; Q. marilandica and Oxydendrum arboreum, in the south. Some species usually occur only in certain situations: Betula lenta on rocky, nonshale areas, and Pinus virginiana at lower elevations, especially on shale. Other species, while not important

throughout the range, are of interest and seem characteristic of pine stands where they occur. Xerophyllum asphodeloides is common in areas P, Q, and 1. Leiophyllum buxifolium is the most important shrub at site Q and a woody Hypericum forms a dense cover on other rocky, high elevation sites. Lilium michauxii is one of the more colorful exceptions to the usual ericaceous lower strata found with the pine.

Vegetational differences between oak and pine stands, apparent from Tables 9 and 10, will be discussed later.

The species occurring with Pinus pungens are not randomly associated with each other. At least some species tend to occur together and tend not to occur when others are present. Correlation coefficients of 1) the presence of the species and 2) the importance rating given the species, with those of all other species, were determined for a number of the more important ones (see Table 12 for a complete list). Positive correlations significant at the 1% level were used to define groups of three or more associated species within the vegetation of the 1966 pine samples. Correlations of presence gave the following groups:

A. Quercus alba (overstory and understory)
Cornus florida
Hamamelis virginiana
Pinus strobus (overstory)

B. Quercus prinus (understory)
Pinus virginiana (overstory and understory)
Vaccinium stamineum

C. Pinus virginiana (overstory and understory)
Gaultheria procumbens
Quercus coccinea (understory)

Correlations of the importance ratings of species in pine stands gave somewhat different results. Group A defined by presence appeared, but lacked Hamamelis. Groups B and C were lacking, but two new groups appeared:

D. Quercus prinus (overstory and understory)
Carya spp. (understory)
Vaccinium angustifolium

E. Quercus coccinea (overstory and understory)
Tephrosia virginiana
Vaccinium vacillans

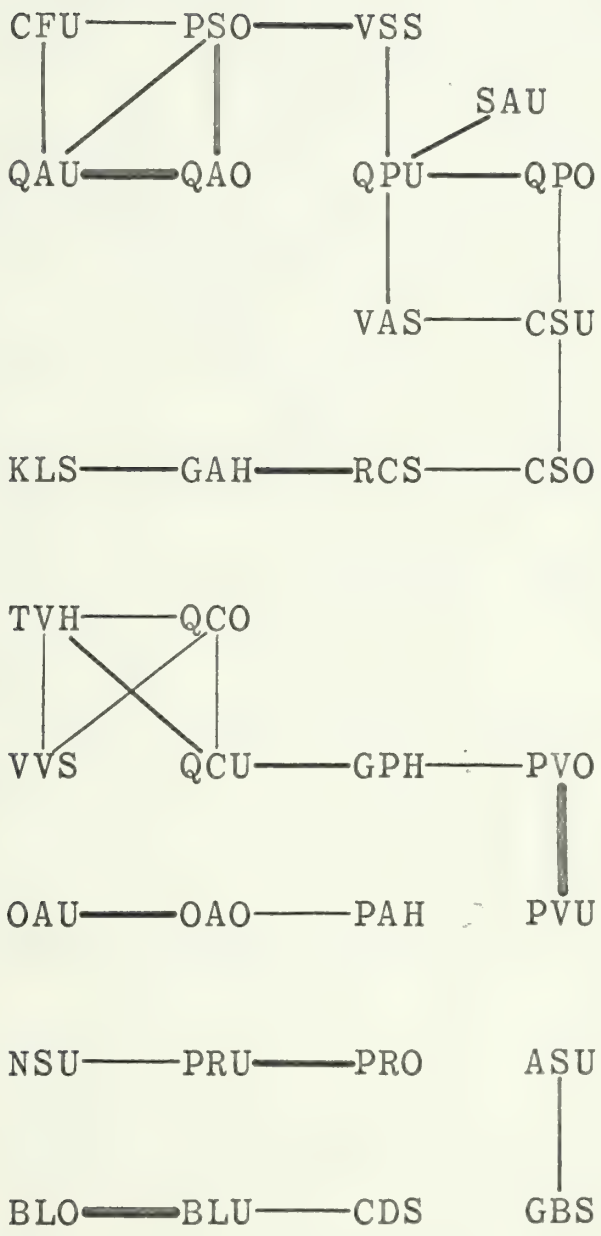
Many groups of two correlated species, or a linear sequence of several, each correlated only to two others, occurred. These indicated the correlation of Galax with Rhododendron catawbiense and with Kalmia latifolia, and of Gaylussacia baccata with Amelanchier spp., for example.

Correlations found within Table Mountain pine stands using the importance rating are shown in Fig. 7, to illustrate

Figure 7. Positive correlations found between importance ratings of species associated with Pinus pungens. Significance level of r (37 d.f.) is .41 for 1%. Species are represented by the following symbols: AS, Amelanchier spp.; BL, Betula lenta; CD, Castanea dentata; CF, Cornus florida; CS, Carya spp.; GA, Galax aphylla; GB, Gaylussacia baccata; GP, Gaultheria procumbens; KL, Kalmia latifolia; NS, Nyssa sylvatica; OA, Oxydendrum arboreum; PA, Pteridium aquilinum; PR, Pinus rigida; PS, Pinus strobus; PV, Pinus virginiana; QA, Quercus alba; QC, Q. coccinea; QP, Q. prinus; RC, Rhododendron catawbiense; SA, Sassafras albidum; TV, Tephrosia virginiana; VA, Vaccinium angustifolium; VS, V. stamineum; VV, V. vacillans. Stratum symbols follow the species symbol. They are: O, overstory; U, understory; S, shrub; H, ground cover.

The degree of correlation is represented as follows:

r	Symbol
$.41 < r < .45$	———
$.45 < r < .55$	———
$.55 < r < .65$	———
$r > .65$	———


CFU
PSO
VSS
SAU
QAU
QAO
QPU
QPO
VAS
CSU
KLS
GAH
RCS
CSO
TVH
QCO
VVS
QCU
GPH
PVO
OAU
OAO
PAH
PVU
NSU
PRU
PRO
ASU
BLO
BLU
CDS
GBS

the basis for groupings listed previously.

Negative associations also provided clues to the species patterns within the range. Presence of Galax was negatively correlated with Quercus prinus (understory), Q. ilicifolia and Vaccinium vacillans, for instance, showing they occupy different geographic areas within the range of Pinus pungens, or that they occur on different types of sites. Negative correlations of importance ratings showed Galax negatively associated with Q. prinus (overstory and understory) and with V. vacillans.

Similar analysis of correlations of species in all stands gave groupings related to the degree of association of the species with pine or oak stands. These will be discussed later.

Importance ratings of species from pine stands were also correlated with some site and soil factors (see Table 11 for a complete list). Correlations significant at the 1% level showed the following patterns of species distributions with respect to the site characteristics examined. After each species is listed the change in the characteristic correlated with an increase in the importance rating of the species. An increase in the magnitude of the characteristic is coded (+); a decrease is coded (-).

A. Overstory trees.

1. *Quercus prinus*: elevation (-), latitude (+), subsoil water holding capacity (+), subsoil nitrate (+), topsoil magnesium (-).

2. *Q. coccinea*: elevation (-).

3. *Carya* spp.: subsoil calcium (+), potassium (+) and organic matter (+).

4. *Pinus strobus*: latitude (+), topsoil organic matter (-).

5. *Q. alba*: subsoil calcium (+).

6. *Oxydendrum arboreum*: subsoil ammonium (+).

7. *Betula lenta*: topsoil calcium (+) and phosphorus (+), subsoil phosphorus (+) and percent rock outcrop (+).

B. Understory trees.

1. *Q. prinus*: elevation (-), latitude (+), subsoil nitrate (+).

2. *Q. coccinea*: topsoil pH (+).

3. *Q. alba*: subsoil gravel (+).

4. *Nyssa sylvatica*: total basal area (+), topsoil organic matter (-), subsoil organic matter (-).

5. *Oxydendrum arboreum*: topsoil water holding capacity (+), topsoil ammonium (+).

6. *Sassafras albidum*: subsoil potassium (-), topsoil gravel (-).

7. *Cornus florida*: total basal area (+), topsoil manganese (+), subsoil manganese (+).

8. *Betula lenta*: subsoil phosphorus (+).

C. Shrubs.

1. *Rhododendron catawbiense*: elevation (+), topsoil organic matter (+) and magnesium (+), subsoil organic matter (+).

2. Kalmia latifolia: subsoil water holding capacity (-).

3. Vaccinium stamineum: elevation (-), latitude (+), subsoil nitrate (+).

4. V. angustifolium: latitude (+), topsoil nitrate (+).

D. Ground cover.

1. Galax aphylla: elevation (+), latitude (-).

2. Tephrosia virginiana: elevation (-).

Correlation does not imply causality. Significant correlations between certain species and characteristics can result from several relationships between them. The plant may respond to the characteristic or to some other characteristic correlated with it, or may determine the characteristic. Using the 99% confidence level, one would expect one percent of correlations to be significant by chance.

The nature of the characteristic can help to define the type of relationship. Presence of a given species cannot influence elevation or latitude of a stand. However, the concentration of some nutrient, especially in topsoil, may be greatly influenced by the vegetation. Several species listed above (Carya spp., Cornus florida, and Quercus alba) accumulate calcium more than other species, as Q. coccinea and pines (Kramer & Kozlowski, 1960). Litter fall concentrates this in the upper soil layers. Selective uptake may also involve exclusion of an element. Gerloff et al. (1966) show

that several species of Cornus in Wisconsin exclude manganese. Cornus florida, which was not studied by Gerloff et al., is positively correlated with higher concentrations of manganese in the pine stands studied. Gerloff et al. suggest that Cornus tolerates high levels of manganese by excluding it, a mechanism which may operate in C. florida, although the species was present in too few stands to give strong evidence for the mechanism.

Despite the dangers of using correlations as a substitute for proof of cause-and-effect relationships, some correlations in the above list are useful for suggesting reasons for the occurrence of groups of associated species listed above. The negative correlation of Quercus prinus (understory) with Galax may be due to opposite patterns of importance in relation to elevation and latitude. In the group of associated species denoted B, Q. prinus (understory) and Vaccinium stamineum showed similar relationships to elevation, latitude and subsoil nitrate levels. In group D, Q. prinus in both strata and V. angustifolium increased with increasing latitude and subsoil nitrate. In group E, Q. coccinea (understory) and Tephrosia virginiana both increased at lower elevations. Importance ratings of some species (Carya spp., Betula lenta, Q. alba, Cornus florida and Rhododendron catawbiense) were correlated with higher levels

of mineral nutrients, but Sassafras was negatively correlated with potassium concentrations, and Q. prinus (overstory) was correlated negatively with magnesium. Several of the species associated with those pine sites with higher levels of certain nutrients are relatively unimportant in pine stands but more common in neighboring oak stands (Tables 9, 10), which have higher average nutrient concentrations (Table 7).

Several workers have described vegetation containing Pinus pungens (Rodgers, 1965, and Racine, 1966, for the southern Blue Ridge; Cain, 1931, and Whittaker, 1956, for the Great Smoky Mountains; Williams & Oosting, 1944, for Pilot Mountain, N.C.; Davis, 1930, for the Black Mountains, N.C.; and Allard, 1946, for shale barrens on Massanutten Mountain, Va.). A compilation of species lists from the above papers showed general agreement with the information presented in Tables 9 and 10. One difference between this study and the previous ones is in the relative importance of Quercus prinus and Pinus rigida. This study showed Q. prinus to be more common, and to be quite important, while five of the studies listed above considered P. rigida the more important. Distribution of study areas explains this discrepancy. Q. prinus is more important at lower elevations and higher latitudes, where many samples of the present study were taken, while six of the seven papers cited above are from North Carolina and

Tennessee. In three of the four 1966 sample areas in these two states, where at least one of the two species occurred, P. rigida was more important than Q. prinus, the same relationship found in the literature.

A few other species cited in at least three of the seven studies, but not in Tables 9 or 10, showed similar relationships, being in less than four southern stands. Two herbaceous species cited in several of the southern studies were not recorded in any stands during this study as separate species. Andropogon spp. were the most important herbaceous species found growing with Pinus pungens by Racine (1966), Rodgers (1965), Whittaker (1956) and Williams & Oosting (1944).

One can extract a good picture of vegetation found with Pinus pungens from Whittaker's (1956) nomograms (in his Appendix A), indicating the relationships between the "Table Mountain pine heath" and a number of species of trees. Importance of tree species occurring with P. pungens in xeric and subxeric sites (Whittaker's Tables 6 and 7) correspond closely to what was found in this study, excepting those species not found in the southern part of the range.

Vegetation similar to that found with Pinus pungens also occurs in other areas. Cain (1931) and Davis (1930) comment on the similarity of the mountain "pine heaths" to Coastal Plain pine barrens. Reiners (1965, 1967) describes

the shrub layer of pine barrens on Long Island as a discontinuous stratum of Quercus ilicifolia above a layer of Gaylussacia baccata, Vaccinium vacillans and V. angustifolium. This group of species was found intact in six of the northern 1966 pine stands, and lacked only one component in 13 more. Thirty-two of the 38 1966 pine stands had at least two of the four species. Canopy species cited by Reiners, especially Pinus rigida and Q. coccinea, were common in many stands of Table Mountain pine.

The vegetation of Table Mountain pine stands is composed mostly of species with wide ranges and apparently wide environmental tolerances, such as Quercus prinus, Q. coccinea, Pinus rigida, P. virginiana, Kalmia latifolia, Vaccinium vacillans, V. stamineum, V. angustifolium, Gaylussacia baccata, Smilax spp. and Pteridium aquilinum. No species could be called exclusive to the stands. The vegetation seems to consist of those species in the local flora which can survive the rigors of the particular site.

Other Biotic Factors. Several biotic factors in addition to higher plants may influence the occurrence of Pinus pungens and characteristics of the stands where it grows. P. pungens is susceptible to a number of insects. One causes an enlargement of the basal portion of the needle

fascicle and very short needles, but the damage was usually limited to a few fascicles on a given branch and seemed of minor importance.

A cone-boring insect may have a more significant effect on the species. Its effects were recorded on six sample areas in 1966, and damage was rated "heavy" at sites N, M, F and E, from Georgia to Maryland. The larva eats the part of the maturing cone between the central core and the outer layer of the cone, destroying the seeds. In some years it appears to destroy the entire seed crop of an area. Damage varied greatly from year to year in some areas.

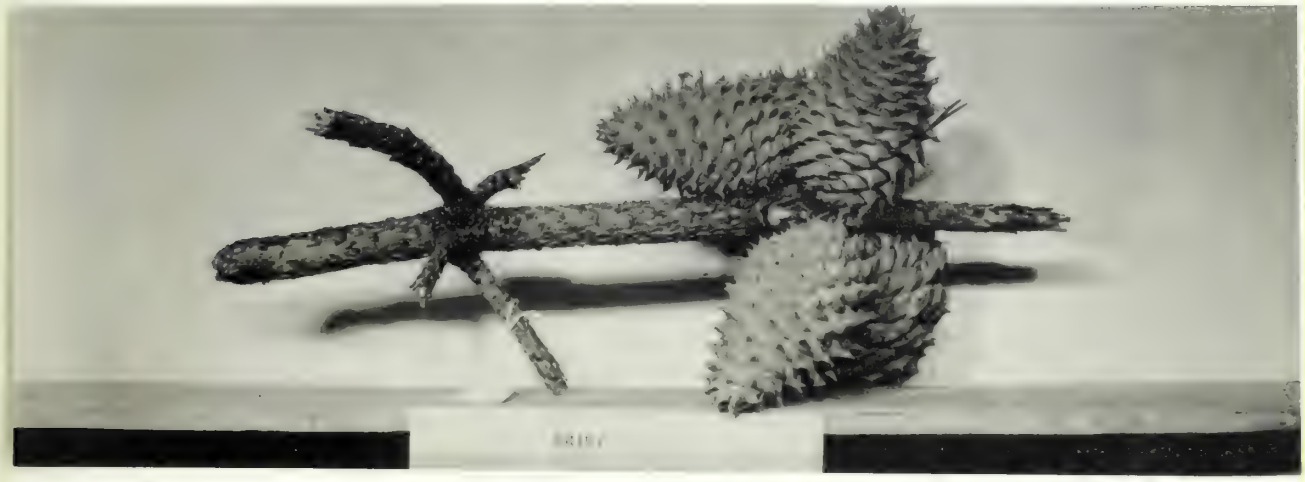
The red squirrel (Tamiasciurus hudsonicus) is another seed consumer. The range of this squirrel encompasses that of P. pungens (Collins, 1959; Golley, 1962). Mollenhaur (1939) attributes the scrubby appearance of Pinus pungens in Pennsylvania to limb cutting by red squirrels, to obtain the cones. Such damage was noted during this study, almost throughout the range of the species. Although the act of branch cutting was never observed, it is presumably done by the red squirrel, which is forced into less desirable habitats by gray squirrels (Gifford & Whitebread, 1951). Squirrels cut branches with closed cones on them, up to an inch or so in diameter, and then remove the cones on the ground by chewing through the branch. The cone scales are removed from the base to the apex of the cone by severing

the base of each scale, leaving piles of scales and cone "cores", along with the branch tips, under the trees. Branches and cones cut by squirrels are illustrated in Fig. 8.

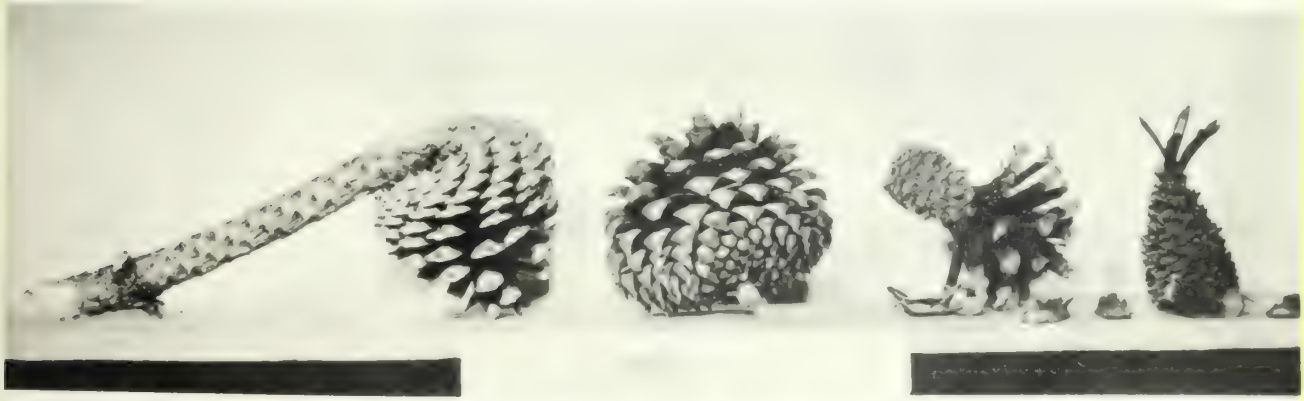
"Squirrel damage" occurred in all 1966 sample areas except N and R. It was light in almost all Valley-and-Ridge province samples and moderate to heavy along the Blue Ridge, especially in North Carolina. At Moore's Knob, Stokes County, N. C., no damage was noticed until the winter of 1966-67, after a spring frost had destroyed the year's acorn crop. In a young stand with no sign of previous damage, being used for phenological observations, almost all branches with closed cones were cut. This indicates the seeds might serve as a reserve food supply for the squirrels. Mollenhaur (1939) says, however, that use of Pinus pungens seeds was not limited to "hard winters" in Pennsylvania. Observations during this study also indicate more common use, since fresh cuttings were seen at all times of the year. Damage to Table Mountain pine results from reduced growth as well as loss of seed supply. The leader and ends of the most vigorous branches are repeatedly destroyed, removing a large part of the photosynthetic surface plus past growth. Reduced height growth and crown expansion decreases the competitive advantage of Pinus pungens relative to those species not

Figure 8

Branches and Cones Cut by Squirrels



a) A branch showing the whorled cones, with greatest development of umbo and apophysis on the side away from the branch, protecting the point of cone attachment. One cone, from the side facing the observer, has been removed.



b) Successive stages, left to right, in harvest of pine seed by squirrels: cut branch, with cone almost removed by chewing through the branch; cone separated; basal scales removed; cone "core" with severed scales.

suffering such trimming. Although red squirrels cut cones of several eastern pine species (Gifford & Whitebread, 1951), in the stands studied damage to other species was almost never seen, especially branch cutting. Squirrels may be able to remove the less heavily-armed cones of other pines from the branch on the tree. Although damage to Table Mountain pine has a marked effect on the form of the tree, it appears to play a somewhat less important role in causing "scrubby appearance" and heavy limbs than Mollenhaur (1939) attributes to it.

Smith (1965) made an intensive study of the relationship of the red squirrel to Pinus contorta in southern British Columbia. Squirrels apparently feed on the highest energy diet available, which is coniferous seed. Although more energy can be gained from other species for a given amount of work, the serotinous cones of P. contorta provide a constant food source. Cones are attacked similarly to the apparent method for P. pungens. Cutting limbs with several cones on them saves energy and allows harvest of whorled cones. Smith proposes that cone characteristics which reduce the rate of energy yield of pine-seed eating are the result of selective pressure by squirrels. Such characteristics include greatly thickened basal scales, spines, and whorled cones protecting the points of attachment

to the branch, sterile basal scales on the cone, and hard scales, all except the first well-developed in Pinus pungens (Fig. 8). The same ideas might apply to it also. Cone cutting by squirrels has also been reported on P. radiata (Forde, 1964) and P. muricata (Duffield, 1951), among other species.

Fungal infection does not appear to be extremely important in the ecology of Pinus pungens. Eastern gall rust (Cronartium quercuum: identification by Dr. W. J. Stambaugh) occurred in one stand. Heart rot is common in older trees in some areas. It appears to enter most often from fire scars and from the long-persistent branch stubs characteristic of the species. Most trees with heart rot, except those deeply fire-scarred, appear to be well over 100 years old.

Fire. Signs of fire were almost ubiquitous in stands of Table Mountain pine. Fire scars, charred bark on living trees, charred chestnut logs, and charcoal buried in the soil indicate fire was an important and relatively frequent part of the environment at some time during the life of the stands studied, as it is for many other pines (Mirov, 1967: p. 444). Whittaker (1956) attributes presence of pine in areas of oak-chestnut climax in the Great Smoky Mountains,

and its single age stand structure and periodic reproduction, to fire. However, he emphasizes that fire is not the complete controlling influence for pine stand distribution.

Age structure of the Pinus pungens stands studied indicates the possible importance of fire. In many stands most of the trees fall into one or two age groups, young trees often growing in thickets with no older ones. In several stands one tree much older than the stand in general occurred on a location where it would be away from the most intense heat of fires, such as at the top of a rocky cliff, or on a rocky point well above the stand below and somewhat isolated from that above. Such trees have apparently served as the seed source for repeated regeneration of the stand after fires.

The vegetation found with Table Mountain pine is often dominated by fire resistant species. Pinus rigida is reputed to be the most fire-resistant species in the northeastern United States, and Quercus prinus is considered second, according to a survey of foresters (Spalt & Reifsnyder, 1962). Bark properties also indicate high resistance for these species. Q. velutina, Q. alba and Q. coccinea are rated next among the species in the range of Table Mountain pine. However, Fowells (1965) cites Q. velutina and Q. coccinea as being quite susceptible to fire,as they have relatively thin

bark. *Pinus pungens* was not rated, but has bark somewhat similar to that of *P. rigida*, although the outer scales are somewhat looser and longer, at times giving it an appearance similar to shagbark hickory.

Serotiny of the cones adapts Table Mountain pine for persistance on sites with repeated fires. It allows the population to maintain the maximum possible seed supply available at all times. Fire, the chief factor which creates conditions allowing the species to colonize new areas, or which destroys existing stands also releases the stored seed.

Cones may remain closed for many years, perhaps 25 (Lamb, 1937). Closed cones were collected during this study, within three to six feet of the ground, from the trunks of three trees with 20 to 30 growth rings at 4.5 feet. Some seed from all three cones germinated. However, cones usually open much earlier. In dense stands, many cones may remain closed 8 to 10 years, but in more open stands usually open sooner.

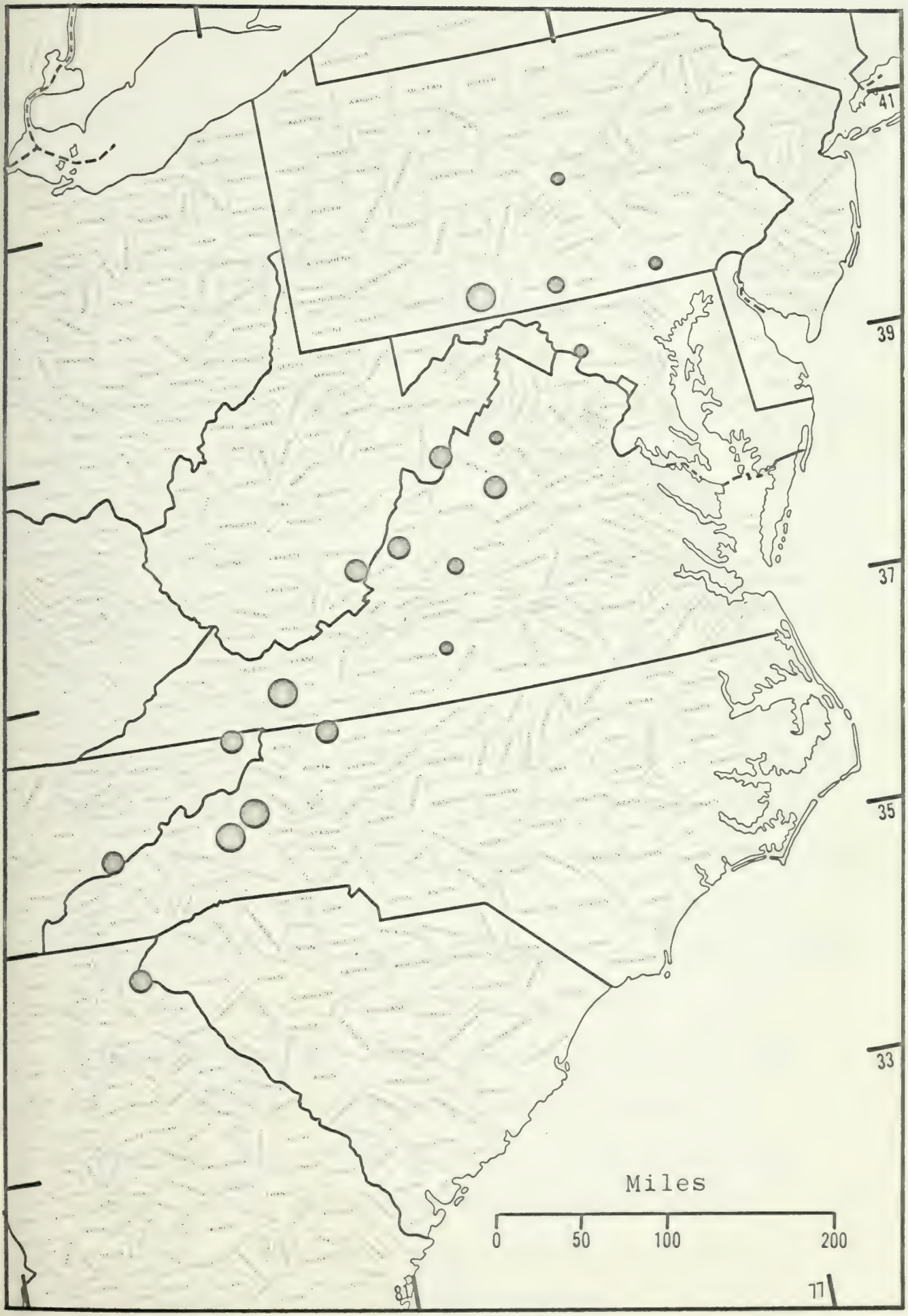
Serotiny varies among trees in a stand, and among different stands. McIntyre (1929), who found a temperature of about 90 F necessary to open cones in Pennsylvania, cites differences in serotiny depending on aspect, stand density,

and shading of cones. Some similar environmental differences in serotiny were observed during this study. Regional differences suggest variation between stands (and probably also some of that within stands) is genetic (Fig. 9). Stands in which most cones opened the first and second years were concentrated in the northern part of the range, where maximum temperatures are presumably no higher than farther south. When serotiny shown on Fig. 5 was coded (Group 1 = -3, group 2 = -1, group 3 = +1, group 4 = +3) and correlated with the same site factors as vegetation (Table 11), it showed highly significant correlations with elevation (positive) and with latitude (negative).

One recently-burned stand was sampled (1965 area 10). All cones were open, even though the fire had been light in part of the area. Regeneration, however, persisted two years later only in areas where the canopy trees were killed and the undergrowth almost completely killed, especially where erosion had exposed mineral soil. This instance suggested that a severe fire is necessary to successfully regenerate Table Mountain pine on sites with a well-developed shrub layer.

Saplings of Pinus pungens may produce cones when 3 to 6 feet tall. McIntyre (1929) suggests five years as a lower age for seed production, and says viability is equal

Figure 9. Cone serotiny in 1966 sample areas. Cones usually open (1) first year (●), (2) by third year (●), (3) by fifth year (●), (4) fifth year or after (●).


41
39
37
35
33
Miles
0
50
100
200
81
77

regardless of tree age. Righter (1939) cites 3 years as the age when "flower" production of both sexes began in cultivation in California. Early reproduction would allow a minimal time without reproductive potential for a newly established stand, aiding persistence in areas with frequent fires. Seeds from a 6-foot sapling from Moore's Knob, Stokes County, North Carolina, at 2200 feet, were tested for germinability. Seeds from the most recent year (1967) showed good germination, although none from cones at 3 feet, the crop of 1965, germinated under the same conditions. This might be a function of juvenility of the tree at the time or some other factor.

Fire, although apparently rare in very recent years on the areas studied, has probably been more frequent in the past, especially from time of settlement until about thirty years ago. During this period, mountain inhabitants burned forest lands for a variety of reasons beneficial to themselves (Freer, 1950). That fire was also a part of the mountain environment before settlement is emphasized by Komarek (1967), who cites instances of recent lightning fires in the Appalachian Mountains, frequent enough to provide a basis for development of fire-caused community types and species dependent on fire for the majority of their reproduction. Fire has probably played a larger role in the history of most, if not all, of the stands studied, as well as in the evolutionary development of *Pinus pungens*.

III. FACTORS DISTINGUISHING TABLE MOUNTAIN PINE STANDS FROM OAK STANDS

Meteorological Observations

Field sampling done in 1966 was designed to determine differences existing between stands in which Table Mountain pine was important and contiguous ones where it was absent or only incidental. Some meteorological measurements were made in many of the stands, as described in an earlier section, to determine the magnitude of differences existing between pine and oak stands.

Air temperature. Maximum and minimum temperatures were recorded at 6 inches and 4-1/2 feet (15.4 and 137 cm) above the ground in all stands of a sample area, and temperatures in each adjoining pine-oak pair were compared. At 4-1/2 feet, the difference (pine - oak) in maximum temperature varied from -3 F to +9 F (-1.7 to +5 C). The average difference for 77 comparisons was 2.3 F (1.3 C).

A "t-test" of the differences of paired observations (Steel & Torrie, 1960: p. 78) showed the 2.3 F difference to be different from zero at the 1% confidence level. If only comparisons with at least one temperature exceeding 85 F (29.4 C) were used, the difference was 2.9 F (1.6 C). At 6 inches, the average difference between pine and oak was 3.6 F (2 C), also highly significant. When only days above 85 F were considered, the difference was 5.6 F (3.1 C). Differences ranged from -5 to +15 F (-2.8 to +8.3 C).

Minimum temperatures at 4-1/2 feet showed no significant difference. At 6 inches, differences (pine - oak) varied from -7 to +3 F (-3.9 to 1.7 C). The average difference of -0.5 F (-0.3 C), indicating pine was colder than oak, was significant at the 1% level. The generally thinner canopy of pine stands, allowing more radiative cooling of the ground at night than the oak canopy, could cause this. The opposite effect would probably occur when the oaks were leafless.

Vapor pressure deficit. Relative humidity in mid-afternoon (1 to 4 p.m.) was measured about 3 feet above the ground, for 36 comparisons in 11 sample areas. A given pair of measurements was made 5 to 10 minutes apart. Vapor pressure deficit (VPD) was calculated for each measurement

from Murphy's (n.d.) tables. Differences in VPD varied from -.0472 to +.2163 inches of mercury. The average of +.0542 inches was highly significant. The VPD difference between pine and oak stands increases as the absolute value of the VPD increases (Fig. 10).

Soil temperature and moisture. Soil temperatures were taken at each soil sample point in most stands. Where it had rained recently, the soil was almost isothermal and the only readings taken were under the litter and at 40 cm. A "t-test" of temperature differences under the litter showed pine being 1.3 C warmer than oak, significant at the 5% level. No other level had significant differences in temperature. There was no difference between the total temperature gradients, from 40 cm to under the litter, of the pine and oak stands.

Soil moisture samples were taken from each stand of 17 sampling areas. Analysis of the differences between paired stands showed oak stands having an average of 1.7% more moisture in the portion of the sample 2 mm or smaller in diameter, significant at the 5% level. The average difference of 1.0% in the total samples was not significant.

The few short-term readings taken during late spring and summer, summarized above, indicate that Table Mountain pine stands have higher maximum air temperatures at

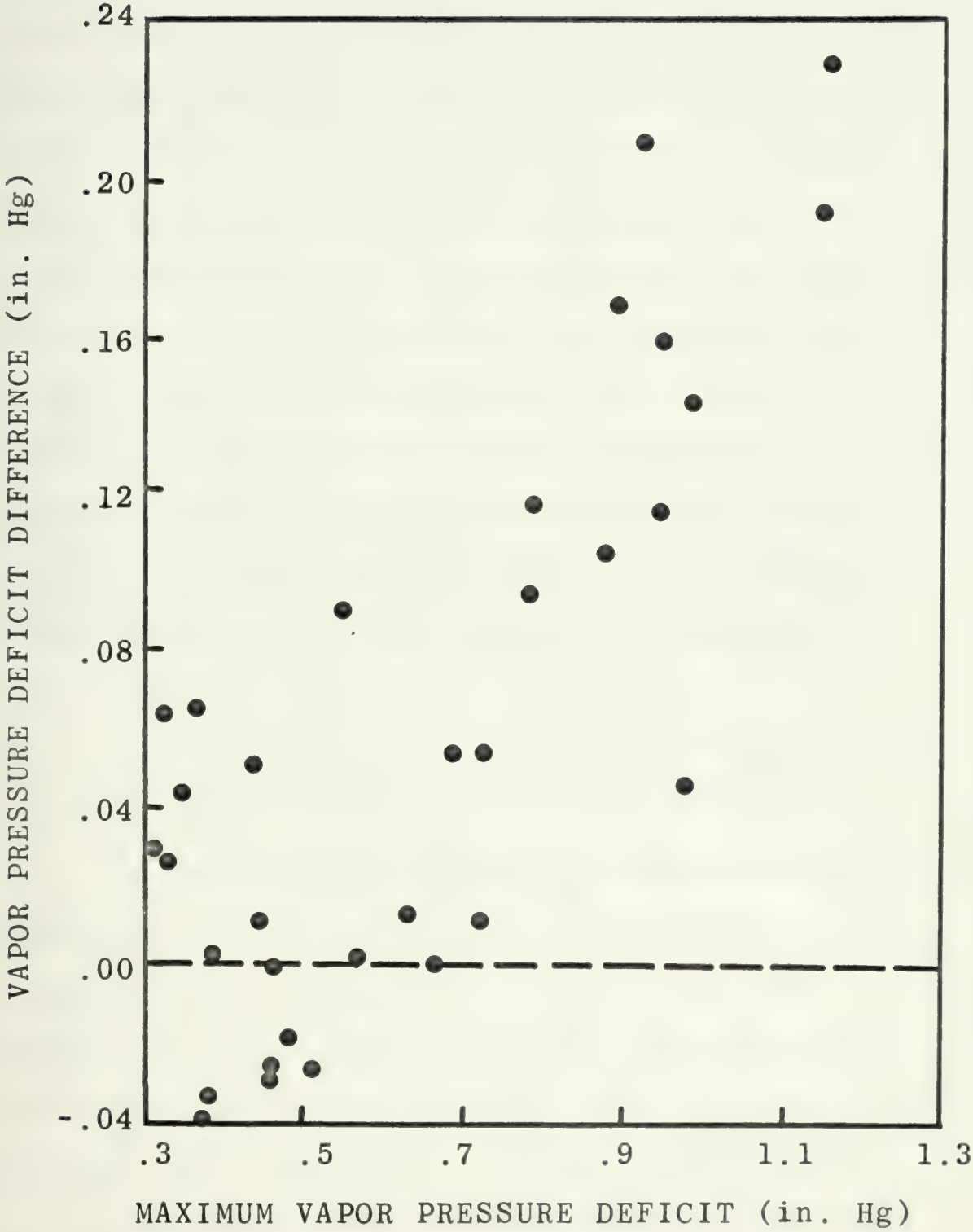


Figure 10. Vapor pressure deficit difference (pine - oak) between pine and oak stands, 1966 sampling areas, in inches of mercury, as a function of maximum VPD encountered in each pair of measurements.

6 inches and 54 inches above the ground, lower minimum temperatures at 6 inches, higher vapor pressure deficits and, perhaps, lower percent soil moisture. These results might be expected from the restricted occurrence of pine stands, centered on the southwestern aspect, while oak stands were sampled on every exposure. Stand differences cited above are similar to aspect differences found by Mowbray (1967) and those cited in Geiger (1965), which were discussed earlier. The soil moisture difference demonstrated may not mean much, because of unknown and variable stone content and soil depth, which could cause much larger differences in total moisture in the soil than the one demonstrated.

Topographic, Soil, and Vegetational Factors

Differences in topography, soils, and vegetation between Table Mountain pine and oak stands sampled in 1966 have been presented (Tables 2, 6, 7, 9, and 10). To determine the significance of differences between pine and oak stands, a discriminant function analysis was used (Williams, 1959: Chapter 10). All Table Mountain pine stands were assigned a "value" of +1; all oak stands were assigned -1. Regression equations were determined with "value" as the dependent variable and various topographic, soil, and

vegetation factors were analyzed separately. Then all variables which had F-values tabulated as being significant in the separate regressions, or which had simple correlation coefficients with "value" which were highly significant, were used to determine combined regression equations. Regressions combining just topographic and soil factors were also determined, to see how well these factors would separate oak from pine sites, disregarding the vegetation. Analyses using all stands, using only the 22 stands on shale, and using only the 54 stands not on shale were done. Vegetation data were analyzed in two ways, first using only presence of a given species in a given stratum, and then using its importance rating.

Tables 11 and 12 list the variables used and indicate which had F-values tabulated as significant in regressions run on groups of factors separately. Correlation coefficients with "value" are listed if they were significant at the 5% level. All topographic and soil variables were assigned values in the terms listed in Tables 2 and 7 except aspect. Aspect in the regression analysis was defined as (Aspect in degrees - 180). Presence of a species was coded as +1; absence was coded as 0.

Stands on shale show better correlation with soil and topographic factors than the non-shale stands. Oak stands

Table 11. Simple correlation coefficients (r) and significance in multiple regressions of "value" of a stand (pine = +1, oak = -1) on site factors. Topographic and soil factors were used in separate regressions. A "+" in the regression column indicates a significant effect of the factor. Correlations are shown only if significant at 5% level or better.

	ALL STANDS		NON-SHALE STANDS		SHALE STANDS	
Factor	r	Regression	r	Regression	r	Regression
TOPOGRAPHIC						
Slope	-.25				-.40	+
Aspect	+.29	+		+		
Elevation						
Latitude						
Potential Solar Beam Irradiation December		+			+.30	+
Potential Solar Beam Irradiation June	+.30	+	+.27	+		
Radiation Index						
TOPSOIL						
Waterholding Capacity (%)						
Litter Depth		+				
Depth						
% Rock Outcrop						
Calcium	-.35				-.55	+
Phosphorus	-.23					

Table 11 (continued)

Factor	ALL STANDS r	ALL STANDS Regression	NON-SHALE STANDS r	NON-SHALE STANDS Regression	SHALE STANDS r	SHALE STANDS Regression
Potassium	-.31				-.49	
Nitrate						
Ammonium						
Magnesium	-.43	+	-.32		-.66	+
Manganese	-.33	+			-.69	+
pH					-.46	
% Organic Matter		+				
% Gravel		+				
SUBSOIL						
Waterholding Capacity						
Calcium	-.27				-.49	+
Phosphorus						
Potassium	-.22					
Nitrate			-.28			
Magnesium	-.31				-.63	
Manganese	-.25					
pH	-.32				-.67	
% Organic Matter						+
% Gravel						

Table 12

Simple correlation coefficients (r) and significance in multiple regressions of "value" of a stand (pine = +1, oak = -1) on species presence and importance rating. A "+" in the regression column indicates a significant effect of the factor. Correlations are shown only if significant at 5% level or better.

	ALL STANDS				NON-SHALE STANDS				SHALE STANDS			
	Presence		Imp. Rating		Presence		Imp. Rating		Presence		Imp. Rating	
Factor	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.
OVERSTORY												
Quercus prinus	-.23		-.57	+			-.55	+			-.65	+
Q. coccinea									.46			
Carya spp.	-.41		-.38		-.35		-.33		-.54	+	-.48	
Pinus rigida	.37	+	.29		.37	+	.29					
P. virginiana	.42		.32		.41		.31	+	.57		.45	
P. strobus										+		
Q. alba												
Oxydendrum arboreum						+						
Betula lenta												
UNDERSTORY												
Q. prinus												
Q. coccinea												
Carya spp.	-.47	+	-.50	+		+	-.45		-.57		-.62	

Table 12 (continued)

Factor	ALL STANDS Presence r	ALL STANDS Presence Regr.	ALL STANDS Imp. Rating r	ALL STANDS Imp. Rating Regr.	NON-SHALE STANDS Presence r	NON-SHALE STANDS Presence Regr.	NON-SHALE STANDS Imp. Rating r	NON-SHALE STANDS Imp. Rating Regr.	SHALE STANDS Presence r	SHALE STANDS Presence Regr.	SHALE STANDS Imp. Rating r	SHALE STANDS Imp. Rating Regr.
P. rigida	.25				.30			+				
P. virginiana	.31		.28		.29				.49	+	.51	
P. strobus												
Q. alba												
Amelanchier spp.												
Nyssa sylvatica										+		
O. arboreum										+		
Sassafras albidum												
Cornus florida	-.37	+	-.35		-.31				-.55			
Betula lenta		+			.30	+		+				
Hamamelis virginiana			-.32						-.46		-.59	+
SHRUBS												
Castanea dentata										+		
Q. ilicifolia	.33	+	.35	+				+	.65	+	.60	
Rhododendron catawbiense		+		+		+		+				
Kalmia latifolia								+				
Gaylussacia baccata	.34		.47		.33		.40				.66	+

Table 12 (continued)

Factor	ALL STANDS				NON-SHALE STANDS				SHALE STANDS			
	Presence		Imp. Rating		Presence		Imp. Rating		Presence		Imp. Rating	
	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.
Vaccinium vacillans (incl. V. pallidum)												
V. stamineum												+
V. angustifolium		+		+		+				+		
GROUND COVER												
Galax aphylla												
Pteridium aquilinum			.30				.26					
Tephrosia virginiana	.45	+	.44	+	.45	+	.43	+	.47	+	.46	
Gaultheria procumbens												

occur on sites with higher nutrient levels, since all significant correlations of the mineral concentrations with "value" were negative. In the vegetation, a few species were significantly different between stand types. Presence alone gave somewhat different results than when the importance rating was used.

Species whose presence is correlated with pine stands are Pinus rigida and P. virginiana in both over- and understory, Quercus ilicifolia, Gaylussacia baccata, and Tephrosia virginiana. Presence of Carya spp. (over- and understory) and Cornus florida are correlated with oak stands. Analysis of importance ratings indicates a similar situation. However, understory P. rigida is not characteristic of pine and Pteridium aquilinum is. Hamamelis virginiana and overstory Q. prinus are correlated with oak stands, but Cornus drops out.

Combined regressions using more than one type of factor gave the results in Tables 13, 14 and 15. Only factors entering the regression with an F-value greater than 2.0 were used.

Factors other than vegetation can account for 83% (R^2) of the variation in "value" on shale sites, but only 25% on non-shale sites and 37% on all sites. All shale stands, when classified using the regression equation by

Table 13

Results of combined regressions of "value" on soil and topographic factors

Stands	Factor	F-value	Multiple Correlation Coefficient (R)
All (n=76)	Aspect	3.10	.61
	Magnesium, topsoil	27.28	
	Manganese, subsoil	5.35	
	Gravel, topsoil	6.93	
	Litter depth	2.70	
	% organic matter, subsoil	2.50	
Non-shale (n=54)	Aspect	8.19	.50
	Potential solar beam irradiation, June	4.86	
	Magnesium, topsoil	2.49	
Shale (n=22)	% organic matter, subsoil	17.68	.91
	Magnesium, topsoil	3.55	
	Manganese, topsoil	16.46	
	Calcium, topsoil	3.21	

Table 14

Results of combined regressions of "value" on soil and topographic factors and species presence

Stands	Factor	F-value	Multiple Correlation Coefficient (R)
All (n=76)	% organic matter, subsoil	7.65	.79
	Calcium, topsoil	11.42	
	Carya spp., understory	20.88	
	Betula lenta, understory	5.01	
	Quercus ilicifolia	13.26	
	Vaccinium angustifolium	10.50	
	Tephrosia virginiana	26.39	
Non-shale (n=54)	Magnesium, topsoil	5.19	.78
	Carya spp., understory	13.20	
	Betula lenta, understory	11.97	
	Rhododendron catawbiense	12.15	
	Vaccinium angustifolium	2.55	
	Tephrosia virginiana	28.68	
Shale (n=22)	*Carya* spp., overstory	25.29	.98
	Pinus strobus, overstory	17.19	
	Oxydendrum arboreum, understory	56.43	
	Quercus ilicifolia	124.18	
	Nyssa sylvatica	17.02	
	Castanea dentata	22.35	
	Vaccinium angustifolium	12.01	

Table 15

Results of combined regressions of "value" on soil and topographic factors and species importance ratings

Stands	Factor	F-value	Multiple Correlation Coefficient (R)
All (n=76)	Magnesium, topsoil	8.81	.80
	% gravel, topsoil	5.04	
	Quercus prinus, overstory	20.33	
	Betula lenta, understory	6.05	
	Q. ilicifolia	2.37	
	Gaylussacia baccata	2.03	
	Hamamelis virginiana	2.50	
	Tephrosia virginiana	19.58	
Non-shale (n=54)	Magnesium, topsoil	2.50	.85
	Quercus prinus, overstory	19.11	
	Betula lenta, understory	16.99	
	Pinus rigida, understory	5.24	
	Q. ilicifolia	6.49	
	Rhododendron catawbiense	9.05	
	Kalmia latifolia	3.11	
	Tephrosia virginiana	34.07	
Shale (n=22)	This regression gave the results shown in Table 13, for soil and topographic factors alone.		

substituting the stand values into the equation, had computed "values" corresponding to what was expected, positive for pine stands, negative for oak stands.

From Table 13, it appears that the differences best separating Table Mountain pine stands from oak stands are topographic on non-shale sites and are related to soil chemistry on the shale sites.

Results with vegetation presence plus soil and topographic factors are in Table 14. These regression equations accounted for 61%, 61%, and 96%, respectively, of the variation in "value" on all, non-shale, and shale stands. When stands were classified using the regression equations, 90%, 87%, and 100% of all, non-shale, and shale stands, respectively, were correct. On shale, no soil factors entered the regression equation with vegetation presence, although shale stands can also be classified by soil factors alone (Table 13).

Use of importance ratings of species gave the results in Table 15. These equations account for more of the variation in "value" than use of presence alone, for non-shale and for all stands. Sixty-four percent of variation in all stands and 72 percent in non-shale stands were accounted for.

Species which are in a small number of stands are most useful in separating pine from oak stands by presence. When importance ratings are used, common species such as Quercus prinus and Pinus rigida are more important, and some less common ones such as Carya spp. and Vaccinium angustifolium drop out of the equations.

Texture of the soil was analyzed for 32 stands from 8 sample areas. Percents of sand, silt, clay and total colloids in sub- and topsoils were included as independent variables with other soil factors, in a regression with "value." None of the textural factors were significantly correlated with "value", although clay in the subsoil was in the regression equation, which had a multiple correlation coefficient of .63, along with subsoil organic matter and topsoil magnesium. Clay was positively correlated with "value", indicating more clay in pine stand subsoils than under oak stands.

Significance levels are not given for the F-values listed in Tables 13-15. The procedure determining the factors used in the combined regression equations (i.e. using regressions of one type of factor to choose which factors of that type to use, and the rejection of all factors with F-values less than 2.0 in the combined equations) does not allow precise statements regarding the significance

of the factors in the equation. Reduction of residual sum of squares by a factor may vary depending on what other factors are in the model with it. Only one of a group of intercorrelated factors may appear in the regression equation even though all are significantly correlated with "value." Some factors may appear because of their correlation with several other factors. The combined regression equations are the ones giving the lowest residual sums of squares possible and are the best obtainable with the method used for classifying stands for presence or absence of *Pinus pungens*, but no exact statement of the significance of the contribution of any variable can be made (M. O. Braaten; personal communication).

IV. "PERMANENCE" OF TABLE MOUNTAIN PINE STANDS

Observation of Table Mountain pine stands shows large differences in the time the stand has apparently existed and the time it might be expected to last. The stand age structure, the amount of pine reproduction and the type of understory vegetation all give clues to what will be called the "permanence" of the stand. Some stands are obviously successional, with one size class of pines, no pine reproduction and a very dense understory of shrubs and more mesic trees. Others have many size classes and essentially no understory, and it appears they will persist for a long time, even without repeated disturbance.

Knowing what factors are associated with "permanence" would further define the conditions to which *Pinus pungens* has adapted. These may be the major conditions under which it will occur at some future time, given no increase in fire and rate of land abandonment.

Identification of factors correlated with "permanence" proceeded as did identification of those associated with pine stands, using discriminant function analysis by regression techniques. First, however, "permanence" had to be operationally defined and stands had to be grouped by their "permanence."

The stand age structure estimated by the increment cores taken from 10 Table Mountain pines in each was used to determine "permanence." (An effort had been made to obtain the age of at least one individual of all size classes present). The number of ten-year age classes represented by the 10 trees was used as one criterion for determining "permanence." A second criterion, called "dispersion", was related to evidence of present and past reproduction by the stand. The range of age classes was divided into quarters (0-30 years, 31-60 years, 61-90 years and greater than 90 years). "Dispersion" values were assigned as follows:

5 = Ages in all four quarters.

4 = Ages in 3 quarters, including the first.

3 = Ages in 2 quarters, including the first, or in 3 quarters not including the first, with *Pinus pungens* seedling importance rating greater than 2.

2 = Ages in 3 quarters not including the first, with seedling importance rating equal to or less than 2.

1 = Ages in 2 quarters not including the first, or in one quarter.

Stands were plotted on a two-dimensional scatter diagram and divided into three groups of about equal size (Fig. 11). Eleven stands with many age groups and showing signs of repeated reproduction, were denoted "permanent." Fourteen, with few age classes and little sign of reproduction, were denoted "temporary." The remaining 15 were considered "indeterminate" and reclassified as outlined below. The 40 groups of trees classified included those from 38 stands plus extra groups of 10 trees each from both stands in sample area C. Both groups from a given stand at C were classified alike. Position of some stands observed to be clearly successional guided placement of lines dividing the stands into groups.

The criteria used to divide stands could include as permanent a stand in which many minor fires caused repeated reproduction without killing the older trees, or could exclude a permanent stand which recently had been almost destroyed by fire, thus having few age classes. These conditions could not be detected in any case, and it is felt that this method objectively separates stands in terms of their age structure, even though division into "permanent" and "temporary" may be somewhat subjective. Some evidence for a meaningful division may be examined by plotting tree height against age for the classified stands.

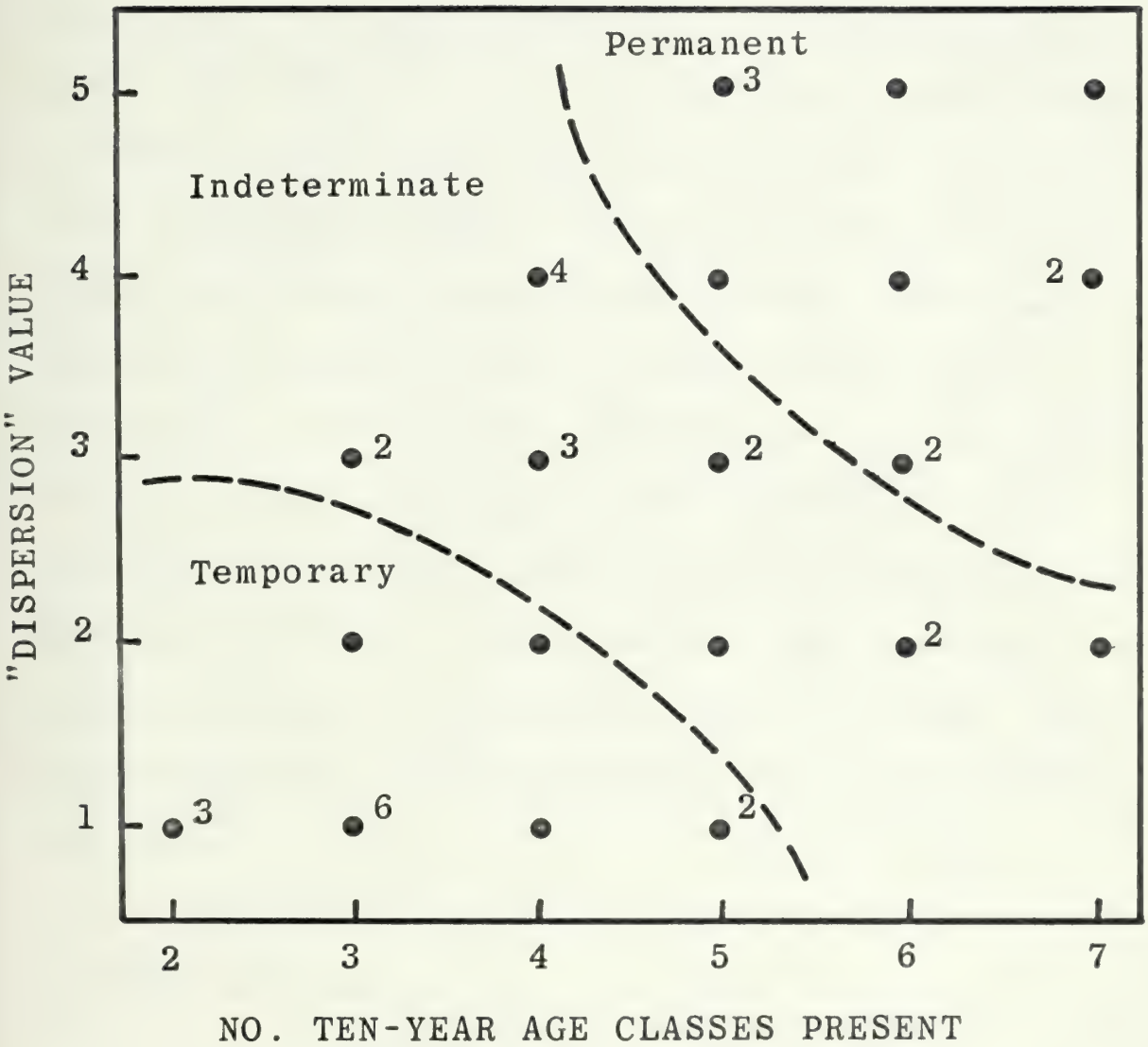


Figure 11. Scatter diagram used to separate stands into "permanence" groupings. "Dispersion" values are defined on p. 96. Numbers refer to the number of stands a given point represents, if greater than 1.

The line for "temporary" stands has a steeper slope than that for "permanent" stands, while values from "indeterminate" stands overlap the variation in both temporary and permanent stands. This indicates a definite difference in conditions in these different types of stand.

The "indeterminate" stands were divided into two groups on the basis of associated vegetation. From a preliminary analysis of species presence, species more characteristic of oak stands than of pine stands were listed. This list was similar to Table 12, but included some less common species not used in the discriminant function analysis. Stands were divided into two groups, six "indeterminate, permanent" and nine "indeterminate, temporary" stands, based on the number of species characteristic of oak stands which were present.

"Permanence" values (referred to as "perm") were assigned as follows:

Permanent stands	+3
Indeterminate stands	
Permanent	+1
Temporary	-1
Temporary stands	-3

Discriminant function analyses equivalent to those with "value" (see previous section) were done to relate "perm" to the factors considered. The same factors, plus six new ones, were used. Ratings for squirrel damage, insect damage to cones, and serotiny; the total stand basal area; and the basal area of Pinus pungens expressed in ft^2/acre and as a percent of the total, were included as "biotic factors."

Tables 16 and 17 list only the factors entering the regressions of separate groups of factors or having significant correlation coefficients with "perm." No regression results are available for soil factors on shale stands due to limited stand number, so only those soil factors correlated with "perm" were used in the combined regression.

Few correlations with "perm" are significant. Permanent shale stands can be said to occur on aspects closer to south than temporary ones, and to have shallower litter and less water-holding capacity in the topsoil of less than 2 mm diameter. Non-shale stands are more likely to be permanent on areas with much rock outcrop and with lower topsoil magnesium. They have less basal area of all species and of Pinus pungens. Several soil properties without significant correlation coefficients also entered

the non-shale regressions.

Few species were characteristic of "permanent" or "temporary" stands. The correlation of presence and importance rating of Castanea dentata with temporary stands may indicate that Pinus pungens filled part of the open niche left by the loss of tree-size chestnuts.

Results of pooled regressions of "perm" with the various factors are in Tables 18-20. Division into shale and non-shale groups of stands resulted in equations accounting for more variation than the equations for all stands. Differences probably do exist between the relationships of Pinus pungens to these two types of sites.

Using vegetation presence, permanent stands on non-shale sites were separated from temporary ones as having less total basal area and less Castanea and Vaccinium angustifolium. Betula lenta and Rhododendron were slightly more important on the more temporary sites and Kalmia on the more permanent ones. The relationships of organic matter and pH to permanence, however, were unclear, as both had low correlation coefficients with "perm." Using importance ratings, permanent stands had less Pinus strobus in the overstory, and less Nyssa and Castanea. The relationships of Galax, Amelanchier, and Oxydendrum to permanence were unclear. Their appearance

Table 16. Simple correlation coefficients (r) and significance in multiple regressions of "perm" (defined on p. 96) on topographic, soil and biotic factors. Groups of factors were run in separate regressions. A "+" in the regression column indicates a significant effect of the factor. Correlations are shown only if significant at 5% level or better. Only factors with significant correlations or effect in regression are listed.

	ALL STANDS		NON-SHALE STANDS		SHALE STANDS	
Factor	r	Regression	r	Regression	r	Regression
TOPOGRAPHIC						
Aspect					-.61	+
TOPSOIL						
Litter Depth	-.47	+			-.80	
% Rock Outcrop	.33		.46	+		
Waterholding Capacity					-.61	
Calcium				+		
Magnesium			-.44	+		
Nitrate				+		
pH				+		
% Organic Matter				+		
SUBSOIL						
Calcium		+				
Nitrate		+				
"BIOTIC FACTORS"						
Squirrel Damage				+		
Total Basal Area	-.43	+	-.51	+		
Basal Area of *Pinus pungens* (ft^2/acre)			-.42			

Table 17. Simple correlation coefficients and significance in multiple regressions of "perm" (defined on p. 96) on species presence and importance ratings. A "+" in the regression column indicates a significant effect of the species. Correlations are shown only if significant at the 5% level or better. Only species with significant correlations or effect in regression are listed.

	ALL STANDS				NON-SHALE STANDS				SHALE STANDS			
	Presence		Imp. Rating		Presence		Imp. Rating		Presence		Imp. Rating	
Factor	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.
OVERSTORY												
Quercus prinus												+
Q. coccinea												+
Pinus rigida					-.39							
P. virginiana				+								
P. strobus			-.32		-.39		-.39	+				
Oxydendrum arboreum								+				
Betula lenta						+						
UNDERSTORY												
Q. prinus			-.32	+							-.74	+
Carya spp.												+
Amelanchier spp.								+	-.69	+		
Nyssa sylvatica							-.39	+				
O. arboreum				+						+		

Table 17 (continued)

Factor	ALL STANDS				NON-SHALE STANDS				SHALE STANDS			
	Presence		Imp. Rating		Presence		Imp. Rating		Presence		Imp. Rating	
	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.	r	Regr.
Sassafras albidum				+								
Cornus florida										+		
B. lenta				+								
SHRUBS												
Castanea dentata	-.36	+			-.52	+	-.57	+				
Rhododendron catawbiense						+		+				
Kalmia latifolia						+						
Gaylussacia baccata										+		
Vaccinium vacillans (incl. V. pallidum)								+				
V. angustifolium	-.44	+			-.48	+						
GROUND COVER												
Galax aphylla				+				+				
Pteridium aquilinum						+						
Tephrosia virginiana	.36		.41	+	.43		.47					
Gaultheria procumbens						+		+				

Table 18

Results of combined regressions of "perm" on soil, topographic and biotic factors

Stands	Factor	F-value	Multiple Correlation Coefficient
All (n=38)	Total basal area	7.08	.69
	Litter depth	14.17	
	Calcium, subsoil	6.21	
	Nitrate, subsoil	6.02	
Non-shale (n=27)	% organic matter, topsoil	8.49	.84
	Nitrate, topsoil	6.91	
	Magnesium, topsoil	18.49	
	pH, topsoil	7.51	
	% rock outcrop	6.40	
	Squirrel damage	3.36	
Shale (n=11)	Litter depth	14.81	.88
	Waterholding capacity, topsoil	5.07	

Table 19

Results of combined regressions of "perm" on soil, topographic and biotic factors and species presence

Stands	Factor	F-value	Multiple Correlation Coefficient
All (n=38)	Total basal area	7.09	.80
	Litter depth	9.74	
	Nitrate, subsoil	2.46	
	Magnesium, topsoil	6.95	
	Castanea dentata	2.93	
	Vaccinium angustifolium	13.26	
Non-shale (n=27)	Total basal area	15.36	.93
	% organic matter, topsoil	6.94	
	Betula lenta, overstory	6.25	
	Castanea dentata	13.27	
	Rhododendron catawbiense	22.16	
	Kalmia latifolia	2.96	
	Vaccinium angustifolium	38.35	
Shale (n=11)	Litter depth	59.46	.99
	Waterholding capacity, topsoil	33.83	
	Quercus alba, understory	3.18	
	Oxydendrum arboreum, understory	64.17	
	Cornus florida	55.62	

Table 20

Results of combined regression of "perm" on soil, topographic and biotic factors, and species importance ratings

Stands	Factor	F-value	Multiple Correlation Coefficient
All (n=38)	Total basal area	12.47	.86
	Litter depth	4.98	
	Magnesium, topsoil	13.27	
	Pinus virginiana, overstory	6.88	
	Quercus prinus, understory	31.64	
	Tephrosia virginiana	14.17	
Non-shale (n=27)	Total basal area	8.32	.97
	% organic matter, topsoil	5.65	
	pH, topsoil	5.94	
	Pinus strobus, overstory	8.53	
	Oxydendrum arboreum, overstory	25.00	
	Amelanchier spp.	22.19	
	Nyssa sylvatica	33.86	
	Castanea dentata	74.47	
	Rhododendron catawbiense	106.48	
	Galax aphylla	31.78	
Shale (n=11)	Litter depth	20.90	.99
	Waterholding capacity, topsoil	71.01	
	Quercus prinus, overstory	7.59	
	Q. coccinea, overstory	34.50	
	Cornus florida	26.74	

in the equation was probably related to correlation with the variation remaining after the data were adjusted for other factors already in the equation.

On shale sites, litter depth and waterholding capacity of the topsoil were both higher in temporary stands. *Quercus alba* and *Oxydendrum arboreum* were somewhat more important in understories of the more temporary stands, although neither was present in many stands. The importance of *Cornus*, present in only two shale stands, was minimal. When importance ratings were used, *Q. prinus* was somewhat more important in overstories of temporary stands, and *Q. coccinea* in permanent ones. *Cornus* was again in the equation.

The combined regression equations involved several variables whose real importance was questionable. However, considerable information can still be gained from those significantly correlated with "perm" and some which have non-significant correlations that are still indicative of their relationship with "perm."

Although many of the factors separating permanent from temporary Table Mountain pine stands were the same ones which separated oak from pine, others were different.

Reclassifying stands using the equations from the combined regression analyses gave the results in Table 21. Only half the shale stands were correctly classified without

using vegetation parameters, but both equations using vegetation factors correctly classified all stands. On non-shale stands, use of soils alone resulted in misclassification of 12 stands; with vegetation presence, seven stands were misclassified, and vegetation importance ratings misclassified only three of the 27 stands. Only the all-stand equation without vegetation factors misclassified a stand by more than one permanence class.

Table 21

Comparison of original "perm" values with those calculated from combined regression equations. Number of stands is given in body of table

	All Stands				Non-shale Stands				Shale Stands			
I. Soil, topographic and biotic factors												
	Original "perm"											
Calculated "perm"	-3	-1	+1	+3	-3	-1	+1	+3	-3	-1	+1	+3
-3	5				3	1			1	1		
-1	6	6	5	2	3	3	1		2	1	1	
+1	2		3	5		2	2	5				1
+3			1	3			2	5			1	3
II. With vegetation presence												
	-3	-1	+1	+3	-3	-1	+1	+3	-3	-1	+1	+3
-3	6	1			5	1			3			
-1	7	4	2		1	3				2		
+1		2	4	6		2	4	2			2	
+3			2	3			1	8				4
III. With vegetation importance ratings												
	-3	-1	+1	+3	-3	-1	+1	+3	-3	-1	+1	+3
-3	9				6				3			
-1	3	6	1			6	2			2		
+1		2	5	5			2				2	
+3			2	5			1	10				4

V. MORPHOLOGICAL CHARACTERISTICS IN NATURAL *PINUS PUNGENS*

Variation Patterns in Cone, Seed, and Needle Characteristics

Specimens of cones and needles were measured to see if any pattern of morphological variation could be detected in *Pinus pungens*.

Needle characteristics. Three needles from each of the three trees were measured for 27 of the 29 areas sampled in 1965. All needle samples were taken from the base of the present year's foliage, from the most vigorous branch collected, and about 10 fascicles per tree were preserved in FAA. Three fascicles were chosen randomly and one needle of each measured. Length, width, and thickness at the center of the needle, number and position of resin ducts in a central cross-section, and number of cells between the vascular bundles were recorded. Analysis of variance was used to determine the significance of variation between sample areas and between trees within areas. Regression

analysis was used to determine the relationship of each character to tree characteristics, such as height, diameter, age, and rate of basal area and height growth (total dimension/number of growth rings).

Variation in all needle characteristics was highly significant between trees within sample areas. Length, width, thickness, length:width index (L/W), number of cells between the vascular bundles ("cells"), and percent and number of resin ducts in an internal position (Harlow, 1931) varied significantly between sample areas. (Length and width were measured in different units, and the values were divided to give the index, which has units of mm/.001 in.) Several of these characteristics also varied significantly with tree height, suggesting an effect of sampling different crown positions depending on tree height. Length, L/W, and total resin canals showed no significant effect of height, however.

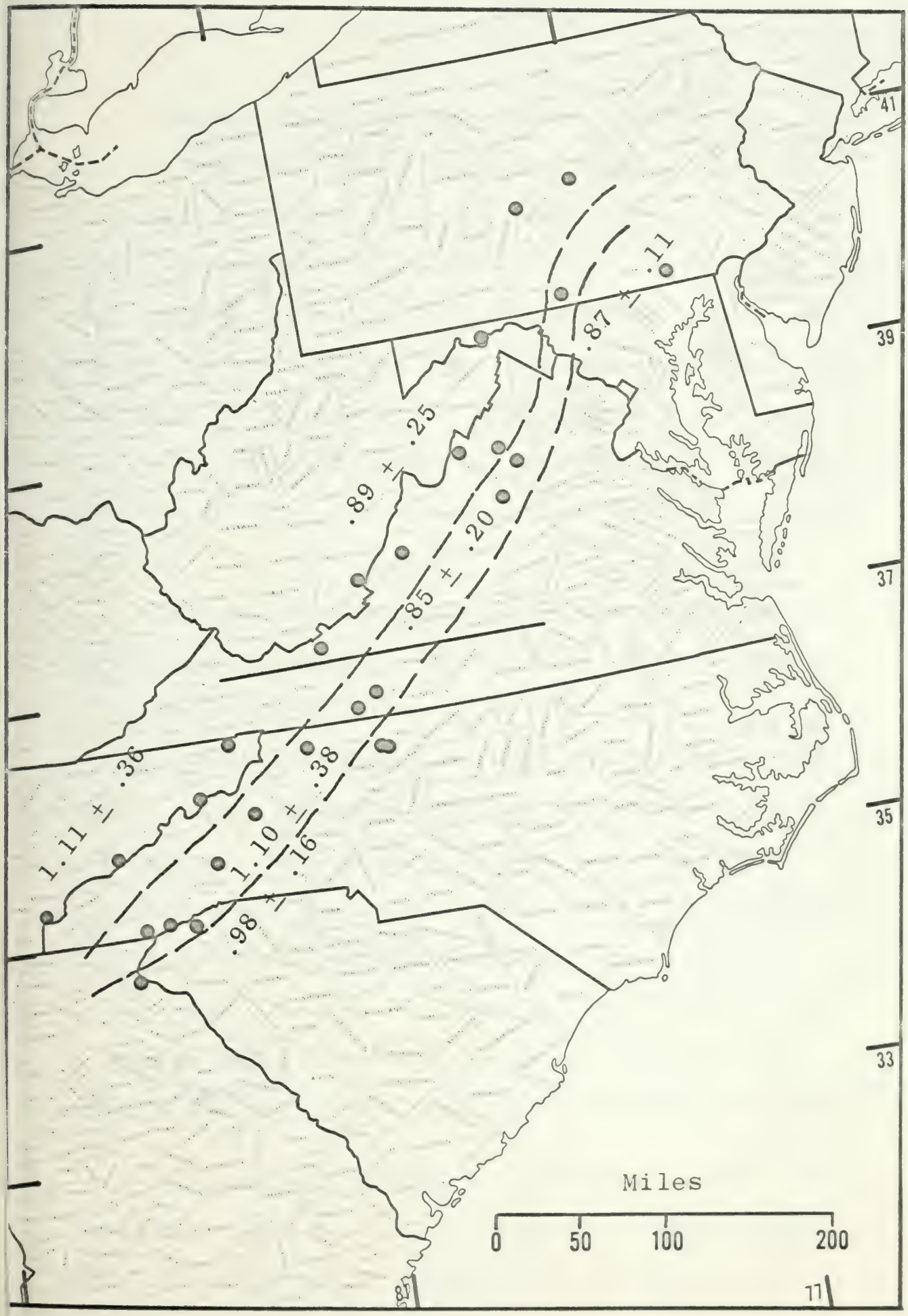
Length, width, L/W, percent internal resin canals, and "cells" were analyzed to see if differences between outlier, Blue Ridge, and Valley-and-Ridge regions were significant. L/W, width, and length were tested for differences between 5 regions: outliers (3 sample areas), Blue Ridge (8), and west of the Blue Ridge (4) south of 37 N latitude; and Blue Ridge (3) and west of the Blue Ridge (8)

north of latitude 37 N. L/W and width were tested for north-south differences, also. When analyzed using tree means as basic data, the L/W difference between north and south was the only regional difference which was statistically significant. L/W just lacked significance in the 5 region comparison. To illustrate the pattern, average L/W for each region is plotted on Fig. 12, with positions of sample areas in each region. The northern outlier was not included in the 5-region analysis. It appears that the needles in the south are relatively more slender than those in the north. A similar but nonsignificant trend occurs from east to west. This is similar to the trend toward longer, narrower needles at lower elevations, in inland sources of Pinus contorta (Critchfield, 1957).

Multiple regressions indicated that length, width, thickness, and "cells" all were higher in trees with faster average growth rates in basal area or height (probably the younger trees). Number of resin canals showed the opposite pattern.

Regression of "cells" and length on site characteristics showed no statistically detectable changes with elevation, aspect, latitude, soil texture or a latitude-elevation variable (COREL = latitude in degrees + 1/100 elevation in meters) which Wiersma (1963) found correlated well with variation in pine and spruce. L/W varied only with longitude (see Fig. 12).

Figure 12. Average needle length:width index ± 1 standard deviation, for 5 regions, 1965 samples. The north-south difference is highly significant.


41
39
37
35
33
85
77
.11
.87 ± .11
.89 ± .25
.85 ± .20
1.11 ± .36
1.10 ± .38
.98 ± .16
Miles
0
50
100
200

Average needle characters from 1965 samples are shown in Table 22A. "Basal" resin canals include those in the corners of the needle and all others along the flat side of the needle. Needle characters are generally similar to ranges cited by Harlow (1931), although maximum resin canal number of 10.7 (tree average) was considerably above the upper limit of 7 he cited. All needles had at least two resin canals, and very few had only the corner ones present. One needle had an external resin canal, a condition not found by Harlow.

Several references, including Harlow (1931), say that Pinus pungens has, rarely or in undefined quantities, three needles per fascicle, as well as two. In this study no systematic effort was made to determine their presence, but only two three-needled fascicles were seen on the 500 or so trees sampled. These were from 4700 feet in the Unaka Mountains and from about 4600 feet at area P. Their presence in these cooler, moister environments corresponds to Haller's (1965) results, correlating increased needle number of Pinus ponderosa with moister years and habitats. One three-needled fascicle was found on a greenhouse-grown seedling.

Cone characteristics. Large variation in cone size, shape and armament occurred both between and within sample areas. The variation is illustrated in Figure 13.

Table 22

Average needle characters, 1965 samples, and cone characters, all collections. Tree means for needle characters are the averages of measurements from 3 needles

Character	Units	n	Mean	Standard Deviation	Range
A Needle					
Length	mm	243	67.8	24.0	33-103
Width	.001 in.	243	68.7	13.2	50-95
Thickness	.001 in.	243	36.7	6.1	27-48
L/W*	mm/.001 in.	81	.99	.34	.62-1.55
Width/thickness*	ratio	81	1.87	.18	1.67-2.11
Total Resin Canals*	no.	81	5.7	3.9	2.0-10.7
Internal Resin Canals*	%	81	18.1	32.0	0.0-55.6
Basal Resin Canals*	%	81	50.0	31.3	26.2-100
B Cone					
Length**	mm	686	71.9	11.0	42-103
Width**	mm	686	53.7	6.6	33-75
L/W**	ratio	686	1.34	.12	.98-1.76
Volume	ml	81	63.8	20.3	26.7-134.0

* tree averages
** data include 1966 samples also

FIGURE 13

Variation in Cone Size, Shape, and Armament

A B C D E F G

a) General variation: A and B. From neighboring trees at area 25, central Pennsylvania; C. Area 29, southern Blue Ridge Escarpment, North Carolina; D. From 3050 feet near Green Bank, West Virginia; E. Area 9, central North Carolina Blue Ridge; F. Area 12, central Virginia Blue Ridge, 3640 feet (see Fig. 1, 16). The terminal scales have not developed. G. Near Newark, Delaware, at 150 feet elevation.

H I J K L M N

b) Local variation: H-L from east slope of Shenandoah Mountain, Rockingham County, Virginia, from elevation of H: 3740 feet, I and J: 3350 feet at area 14, K and L: 2500 feet. M and N from southern Blue Ridge Escarpment: M at 2800 feet at area 29, N from 4250 feet at area 28.

Length and width of closed cones collected in 1965 and 1966 were measured. Total length was defined as the distance between parallel planes, at right angles to the axis of the cone, which just touched both ends of the cone. Width was the distance between the planes when the plane of symmetry of the cone was parallel to the two planes. These measurements include the spines, and differences in spine weathering with age may affect results slightly. However, the most recent cones available were used, and this error should not change conclusions presented here. Cone length, width and length-width ratio (LWR) also include a factor dependent on the size and orientation of the protruding umbo and apophysis ("spine") characteristic of the species. Some cones had large spines which, from the base to the middle of the cone, were reflexed, adding little to width. Width of other cones, with spines at right angles to the cone axis, was considerably increased.

On 1965 cone samples, a "symmetry index" was also determined. Distance from the apex of the cone to the center of the attachment point of the peduncle was measured on both sides, in the plane of symmetry of the cone. A string was stretched as tightly as possible between the end points and then distance measured on the string. The larger distance was divided by the smaller to give

the index.

Volumes of 81 open cones collected in 1965 were determined, by water displacement (Critchfield, 1957). Phyllotaxy of the cone was used to estimate the scale number of several hundred cones collected in 1965. By identifying a secondary spiral, the 1-14-27 parastichie, and counting the number of scales on it, one can estimate the cone scale number, since the number of such spirals is constant on cones with a given phyllotaxy (Duffield, 1951; Forde, 1964a). The direction of this spiral was determined and number of scales on it counted.

Cone length, width, and LWR were analyzed using multiple regression techniques. Each cone of 581 was treated as an individual observation, having all attributes of the site and tree from which it came, and analysis run on cone characters against elevation, latitude, and a combined index of latitude and elevation (COREL), and tree diameter and height, and age. Elevation, COREL, and latitude all significantly reduce variation in length, width, and LWR. Elevation and COREL do about an equally good job when used alone. When site and tree characters are used together, regression of length is significantly affected by functions of elevation, latitude, tree age and diameter. Width and LWR are also affected significantly (5% level) by tree height.

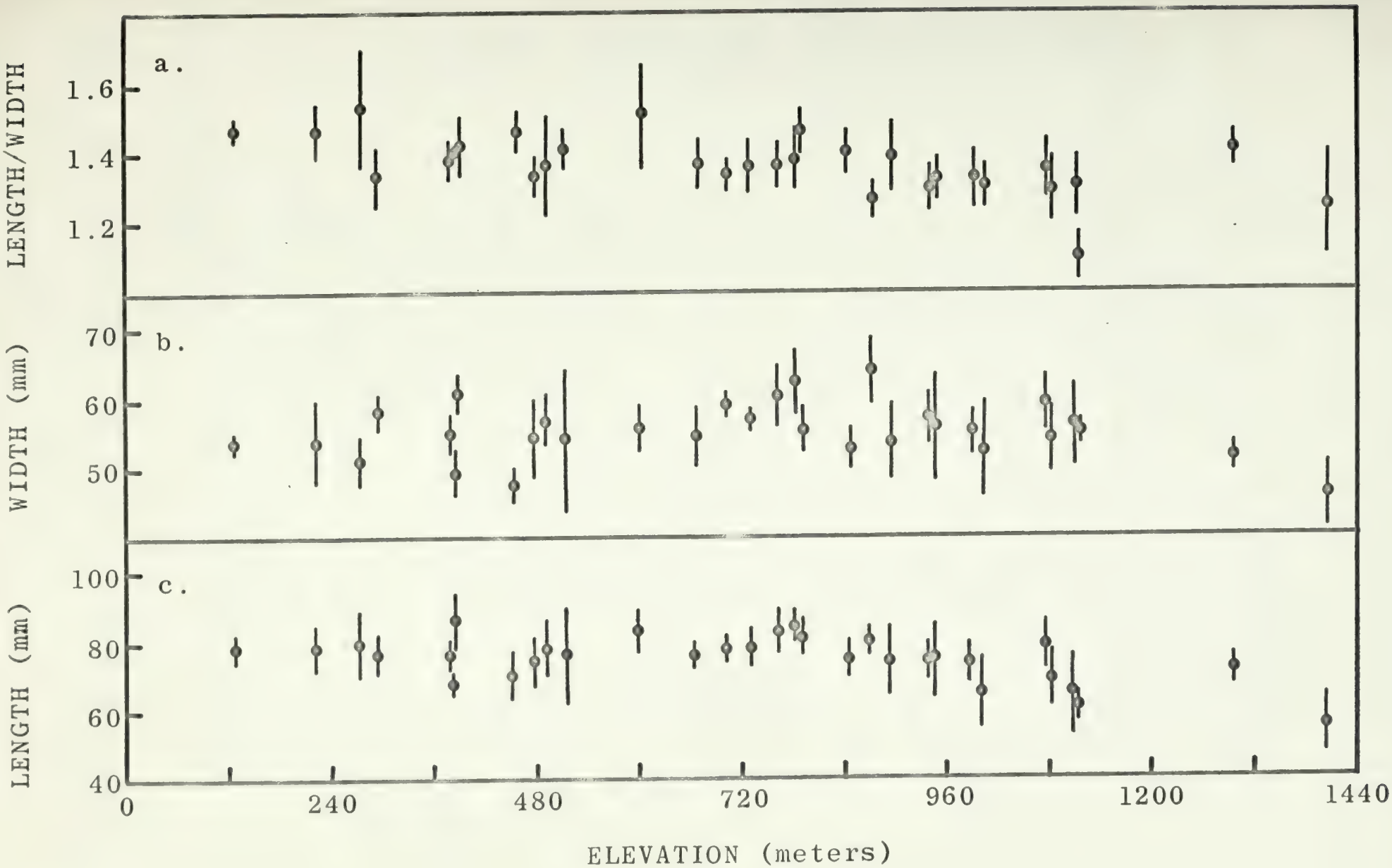
From simple correlation coefficients, it appears that cone length, width and LWR decrease with elevation and COREL, but increase with latitude. The effects of tree measurements are hard to interpret, since tree size is correlated with site factors. The effect of elevation, which accounts for more variation than COREL and latitude, is shown for length, width and LWR in Fig. 14. Only sample areas from which over 5 cones were measured are plotted. It should be recalled that elevation and latitude of sample areas are correlated ($r = -.7$) with no high elevation samples from the north and few low elevation samples from the south.

Cones from high elevations were usually smaller in all dimensions than the lower elevation cones. However, an extremely low LWR (one cone LWR = .98) in area 12 was partly due to poor development of apical scales of the cone.

The symmetry index, measured on only 1965 samples, varied from 1.00 to 1.67 on individual cones, and area averages varied from 1.20 to 1.36 for areas from which 5 or more cones were measured. No general trends with latitude or elevation are evident among these 17 areas.

Cone volumes varied widely, but the range of variation, from 27 to 134 ml, was found within area 25. No geographic pattern was noticed from the small number used, except that highest elevations tended to have small volumes.

Figure 14. Variation of cone a) length:width ratio, b) width, and c) length, with elevation. Mean ± 1 standard deviation is plotted for all sample areas for which more than 5 cones were measured.


a.
b.
c.
LENGTH/WIDTH
1.6
1.4
1.2
WIDTH (mm)
70
60
50
LENGTH (mm)
100
80
60
40
0
240
480
720
960
1200
1440
ELEVATION (meters)

Number of scales counted on the secondary spiral varied from 8 to 17 on 757 cones, averaging 12.0. When sample area means were averaged, Pennsylvania (4 areas) averaged 11.0, between North Carolina and Pennsylvania (13 areas) averaged 12.0, and from North Carolina south (13 areas) averaged 12.2. The Pennsylvania mean differed at the 5% level from the other 2 regions, when intra-area variation was disregarded. It appears that, in the north, cones may have slightly fewer scales. Both directions of spiral are common on cones. Fifty-five percent of the cones are what was defined as "left-handed." Individual sample areas have 26 to 88 percent "left-handed" cones, but direction appears to vary more on a tree-to-tree basis than from area to area. No statistical tests were done.

Table Mountain pine cones are commonly described as sessile (e.g. Hough, 1924). However, the young ovulate strobili and yearling cones have a peduncle about a centimeter long (Sargent, 1897) which usually can still be seen when the cones first mature. This is obscured as the branch diameter increases, causing cones of past years to appear sessile.

Average and extreme values for some cone characteristics are shown in Table 22B.

Seed characteristics. Seeds of *Pinus pungens* vary widely in color, shape, size, and seed-coat texture. Most seeds are roughly triangular and mottled dark-brown or dark-gray to almost black. However, some trees have seeds which are light tan or light with dark mottlings. The seed coat may be smooth or have 1 to 3 longitudinal ridges. Some have wart-like structures, sometimes associated with the dark mottling. In extreme cases, most of the seed coat is covered by this outer layer.

Seeds collected in 1965 were sampled, two 20-seed lots from each tree weighed in bulk, and were scored for color, roughness (amount of warty structure on the seed coat), and ridges, comparing them with a set of "standards" chosen to represent each level of each condition. Seed color was rated 1 to 5 for tan, light brown, dark brown, dark gray, and very dark gray. Roughness and ridges were rated by the amount of the character present, from 1 to 5, and from 1 to 4. Some lots of seed collected in 1966 were weighed, with four 25-seed lots from each tree.

Forty-two of 70 seed lots rated for color were very dark gray (class 5). Sixteen, eight, three and one lot, respectively, were in classes 4, 3, 2, and 1. Class 1, tan, was found at area 14, where classes 3 and 5 were also present.

No overall geographic or elevational pattern in seed color was evident.

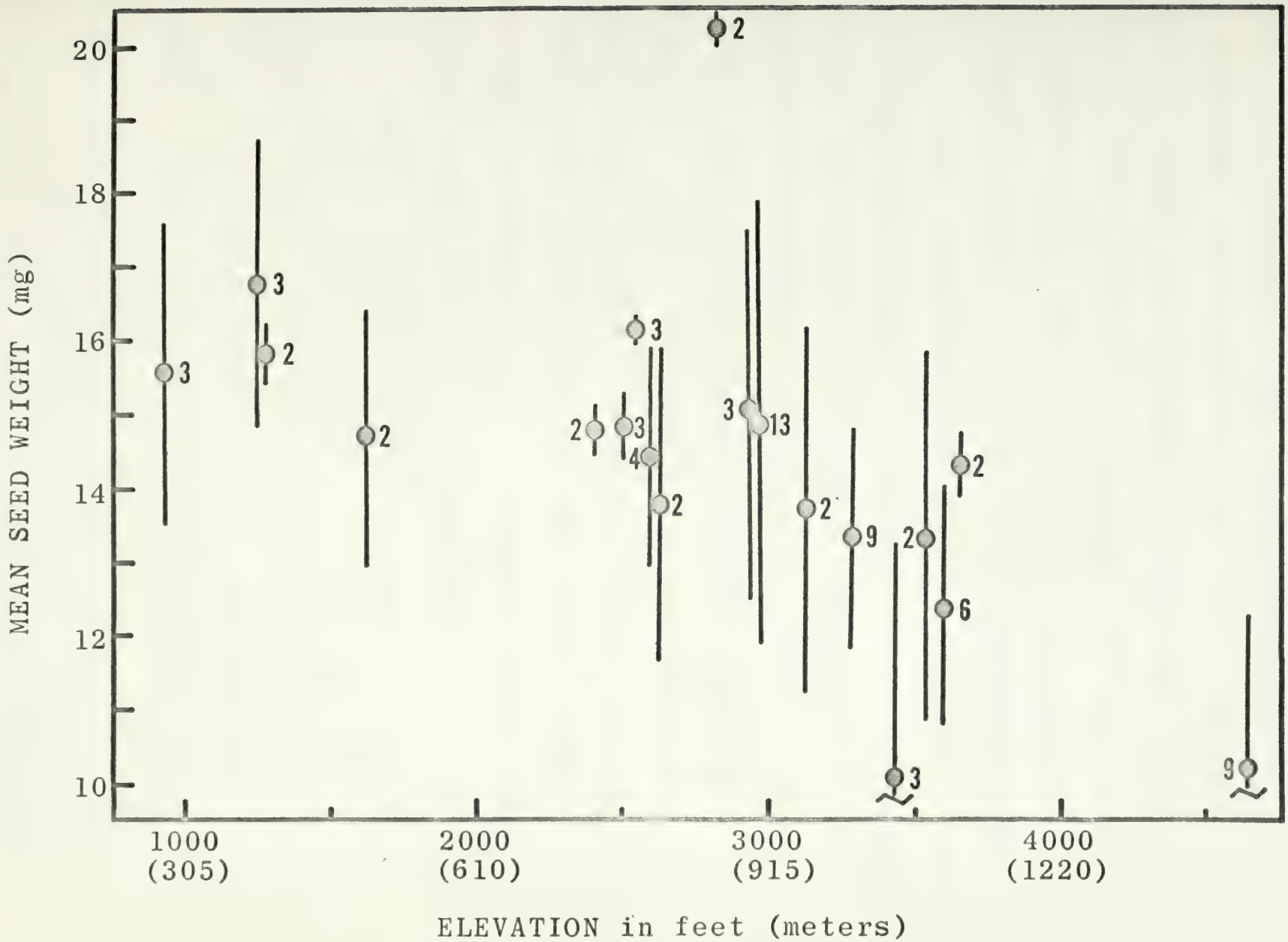
Roughness also showed no particular pattern. Groups 1 and 4, and 2 and 5, were present at the same sample areas. Forty of 70 lots were rated 3, 17 rated 2, 9 rated 4, and 2 each rated smooth and very rough.

Fourteen of 70 seed lots had no ridges, 25 had one, 30 had two, and one had three ridges. Seed lots from south of Virginia had somewhat fewer, on the average, than those northward, but any statistical difference is unlikely.

Tree averages of weight per seed varied from 7.8 to 20.4 mg. The average seed weight from the 13 sample areas for which seed from three or more trees was weighed was 13.8 $\pm$ 2.1 mg. Seed weight appears to be related to elevation (Fig. 15). The heaviest seed was from area 3, a roadside stand where the young pines were exposed on one side and were extremely vigorous. The relationship is better for the more natural stands. Seed size variation parallels cone size, as found for *Pinus radiata* (Forde, 1964a) and *P. sylvestris* (Ruby, 1967). The latter species had largest seeds and cones in drier areas, analogous to the elevational gradient found in *P. pungens*.

Seed of *Pinus pungens* is larger than that of *P. rigida* and *P. virginiana*, averaging 36,000 to a pound (range 29,000

Figure 15. Mean seed weight for areas for which seed from 2 or more trees was weighed, $\pm$ 1 standard deviation, as a function of elevation. Number of trees in each mean shown beside the mean.


MEAN SEED WEIGHT (mg)
20
18
16
14
12
10
1000
(305)
2000
(610)
3000
(915)
4000
(1220)
ELEVATION in feet (meters)
2
3
3
2
2
3
2
3
4
2
3
13
2
9
3
2
2
6
9

to 41,000), compared to 62,000 (36,000 to 83,000) for P. rigida and 53,000 (40,000 to 75,000) for P. virginiana (U. S. Dep. Agr., 1948). Weights of experimental seed lots showed a similar difference. P. pungens seeds from area 4 and Smith Mountain averaged 13.8 mg. each (10 trees), while P. rigida averaged 10.2 (4 trees) and P. virginiana averaged 9.3 (3 trees). These figures are equivalent to 32,900, 44,500 and 49,300 seeds per pound. The difference between P. pungens and the other species, significant at area 4, was much greater at Smith Mountain.

Some of this seed-weight difference could be in a thicker seed coat. Two 10-seed lots of each species from area 4 and Smith Mountain were weighed in bulk, their seed coats removed, and weighed again. The female gametophyte and embryo accounted for 56.3 $\pm$ 3.5 percent of seed weight in Pinus pungens, 64.1 $\pm$ 1.1 in P. virginiana and 60.8 $\pm$ 1.7 in P. rigida. The weight without seed coat was larger for Table Mountain pine (76 $\pm$ 5 mg per 10 seeds) than for Virginia pine (56 $\pm$ 1 mg.) or pitch pine (63 $\pm$ 6 mg.), so some of the seed-size difference is in embryo and food-storage tissue. Large seeds might have adaptive value in drier regions, as proposed for P. sylvestris by Ruby (1967). This would allow P. pungens some advantage in establishing its seedlings quickly. The other species from these sites

have seeds considerably larger than the average size cited above (U. S. Dep. Agr., 1948), also.

Seed measurements made on 10 seeds each from six trees of Pinus pungens agree with seed length of about 1/4 inch quoted by Sargent (1897). They averaged about .14 to .15 inches wide.

Seed wings vary in size and color, similarly to the description for P. radiata (Forde, 1964a). Color may range from transluscent light-tan to dark, opaque brown. Most are intermediate, with varying proportions of dark longitudinal stripes and dark borders, especially at the end distal to the seed. No effort was made to determine how wing characteristics vary with site location and characteristics.

Other Species Characteristics

Tree size and form. Pinus pungens typically has long, thick limbs, covering much of the trunk. On some steep rocky areas these may extend laterally along the ground a distance greater than the height of the tree. It is a poor natural pruner. Even in closed stands, where its branches are relatively smaller and more limited to the upper trunk, it retains branch stubs for a long time. During

1966 sampling, estimates were made of the length of the live crown and of the length of the bole without branch stubs ("clear length"), as a percent of tree height. Average live crown percentage for the 10 trees of each subsample Table Mountain pine stand varied from 38 to 85, averaging 62 percent overall. Clear length varied from 0 to 52 percent, averaging 12 percent. The smallest average live crown, 38 percent, was in the old field at area C. These trees, which averaged 79 growth rings at 4 1/2 feet and 66 feet tall, had a clear length of 28 percent. The more open shale slope stand at area C averaged 106 growth rings, 48 feet tall, 59 percent live crown and 29 percent clear. Greatest clear length, 48 percent, was in area B, which averaged 102 growth rings. In only 7 stands was more than 20 percent of the average trunk clear, and all these averaged over 65 growth rings. Much of the production of this species appears to go into branches. The persistence of live branches and branch stubs causes problems in harvesting, causes "invariably knotty" wood (Grimm, 1950), and provides a pathway for penetration of fungi into the trunk, all reducing the commercial value of the species. Clear wood is produced only after several decades of growth.

Trees of this species often have very crooked, irregular trunks. A characteristic form in older stands

has large branches mostly on the downhill side of the crown, apparently caused by shading from the downhill side of the tree or from the trees upslope (see Frontispiece). The weight of these large branches causes the tree to lean considerably, resulting in production of much compression wood and a trunk cross-section elongated in the direction the slope faces.

Older trees tend to be flat-topped. Form on young trees can be from that of a large bush when open-grown (see Fig. 16) to slender with relatively small limbs, when in a dense stand.

There have been several claims of "largest" trees published (Illick, 1928; Coker & Totten, 1945; Dixon, 1961; Stupka, 1964). The largest measured diameter, cited by Coker & Totten (1945) for a tree 61 feet (18.6 m) tall, cut near Highlands, North Carolina, is 2 feet, 10-1/3 inches (94.4 cm). However, Pinchot & Ashe (1897) cite 3-1/2 feet as an upper diameter limit for the species. During this study, trees over 15 inches in diameter were found occasionally. The largest DBH found was 23 inches (58.4 cm), on a 39-foot tree along the Skyline Drive near area F. A 62 foot tree, 22.7 inches in diameter, and a 71 foot tree, 21.9 inches, grow in Hanging Rock State Park, North Carolina. A 23 inch tree at Mont Alto, Pennsylvania, apparently holds the published height

Figure 16. A Table Mountain pine, at 3640 feet on the Blue Ridge, Shenandoah National Park, Virginia, showing extreme development of open-grown form. The "tree" is about 13 feet tall, 8.4 inches diameter 2 feet above the ground, and has 22 growth rings at 2 feet. A closeup of a branch is in Fig. 1.

record of 73 feet (22.2 m) (Illick, 1928). The tallest tree found in this study was about 95 feet (29 m), and 19.5 inches DBH, at area N. The old field at area C had two trees over 85 feet, and five of twenty were over 70 feet tall.

A maximum age of 250 years (Deen, 1937) appears reasonable for the species. Heart rot prevented age determinations for many large trees. Two trees, near area 28 in a stand dominated by Tsuga canadensis, which were about 15 and 18.9 inches DBH, had 227 and 205 growth rings, respectively. Few other sampled trees approached 200 rings.

Table Mountain pine wood is said to be light, brittle, weak, coarse-grained, soft and knotty (Sargent, 1897; Hough, 1924; Dallimore & Jackson, 1954; and others). Specific gravities of .44 to .59 are cited (Lamb, 1937; Sargent, 1897; Deen, 1937).

Cotyledon number. The number of cotyledons for Pinus pungens is given as six to eight (Loudon, 1844), usually six (Sargent, 1897). In experiment D (see Chapter VIII), the cotyledon number of all sources was counted for both 1966 and 1967 plantings. Pinus pungens had between four and eight (one seedling with nine cotyledons was found from area 10, in a smaller planting). Means for progeny from single trees (based on 42 to 78 seedlings) varied from 5.2 to 6.4. The

means for the three trees from area 4 were 5.5, 6.3 and 5.3, showing almost the total variation found.

Other characteristics. One of the striking features of *Pinus pungens* is the reddish-purple coloration of the mature microsporangiate strobili. The pollen is also of note, being the largest among the eastern North American pines (Whitehead, 1964).

Description of other morphological features may be found in many dendrological books, such as Sargent (1897), Lamb (1937) and others cited earlier in this section.

Evidence of Hybridization

A few sampled trees had some characters intermediate between *Pinus pungens* and *P. rigida*. However, most of these had only intermediate cone characters. One exceptional tree, on Pisgah Ridge in Henderson County, North Carolina, had needle characteristics of *Pinus pungens*, but the one cone sampled was intermediate in size and development of the apophysis and umbo. This tree had a dense group of short, small diameter branches about 15 feet up, which appeared to have originated as sprouts on the trunk, characteristic of *P. rigida*. Others, at area Q and from Smyth County, Virginia,

have foliage like P. pungens, and small cones with moderately well-developed apophyses and umbos. A tree from area M resembled P. rigida, but had thickened scales and somewhat enlarged umbos near the base of the cone. These intermediate trees were rare, but suggest that hybridization, which is genetically possible (Critchfield, 1963), is occurring naturally to a small degree.

VI. PHENOLOGICAL STUDIES

Growth patterns of trees vary with species, in time of growth initiation, length of growing season, and length and timing of the period of maximum growth rate. Different parts of trees grow in different patterns, and the relationship of the several growth patterns within a tree may also vary with species (Kramer & Kozlowski, 1960; Mowbray, 1967). Mowbray found three patterns of diameter growth in the nine species he studied. One pattern included diffuse-porous hardwoods, which dominated the bottomland. The other two included ring-porous oaks and *Pinus rigida* which were most important on the upper slopes. This spatial coincidence of species importance and type of growth pattern suggests that a particular growth pattern is advantageous in certain habitats.

Some phenological differences between *Pinus pungens* and the species with which it competes may exist. This could influence its distribution by allowing it an advantage

on the sites where it is found, or by being disadvantageous on habitats where it is rare or absent.

The most obvious such difference is that between the evergreen pine and deciduous hardwoods. The evergreen habit could allow the species to carry on photosynthesis during favorable weather at any time of the year. Even during winter, branch temperatures on sunny slopes may rise well above air temperatures. Rates of photosynthesis in Pinus ponderosa in Arizona are much higher during favorable winter days than during the hot, dry midsummer, and Fritts (1966) suggested that lower elevation trees in the southwestern United States may accumulate most of their food reserves during the cooler part of the year. Although Pinus pungens occurs in a moister, cooler climate, the same phenomenon could allow it to complete much of its assimilation while hardwoods are leafless and competition for soil moisture is minimal. The longer photosynthetic season could compensate for conditions limiting maximum rates on the nutrient poor, relatively dry sites. This advantage would be greatest in situations with maximum winter irradiation and temperature, those on which Pinus pungens usually occurs (Figure 3; Table 3; Geiger, 1965: p. 421). However, this effect is probably reduced somewhat by chloroplast disruption in the winter, as found in Pinus taeda and some other evergreens (Perry &

Baldwin, 1966). Monk (1966b) found evergreenness to be more important on dry, sterile sites than on the moister, more fertile sites in northern Florida. However, he attributes the difference to a more closed mineral cycle in the evergreen community.

The above discussion could apply to any evergreen species, several of which occur commonly with Pinus pungens. To gain more species-specific information, phenological measurements were made during 1966 and 1967 to determine if any differences existed between Table Mountain pine and some other trees with which it grows.

Twig Elongation

During the spring, 1966, and spring and summer, 1967, twig growth of several species was measured at Hanging Rock State Park, Stokes County, North Carolina (see Fig. 3). At four stations established in February, 1966, twigs were tagged and initial measurements made. A number of trees with accessible branches were used in each area. The leader, two upper and two lower branches of seedlings and small saplings were used. On larger trees, two of the healthier lower branches and two branches in the highest whorl that could be

practically measured were used. Measurements were made from the base of the old bud to the tip of the new shoots, to the nearest millimeter. Information regarding individual trees is in Table 23. When possible, the same trees and same twigs were used both years. Branch-cutting by squirrels, ice breakage and choice of non-vigorous branches necessitated changing some branches and trees in 1967. The "upper point" station was abandoned and two new trees added to the top station in 1967. Records of some individual branches and trees which grew poorly (less than 2 cm elongation per year), or were lost before the end of the season, were left out of the analysis.

In 1966, twig length was measured about every two weeks (13-16 days) from February 27 to May 8. A final measurement on August 2 defined "total elongation." In 1967, measurements were made on February 23, every 14 days from March 11 to May 20, on June 10 and August 2. The only difference between the August 2 measurement and actual total annual elongation was slight bud elongation occurring throughout the late summer and fall. Only a few trees (a seedling of Pinus virginiana and some hemlocks) had more than one flush of growth. The August 2 measurement was made to the tip of the first flush in these cases.

Since the timing of growth was the information

Table 23. Characteristics of sites and trees used in phenological measurements, Hanging Rock State Park, Stokes County, North Carolina. Use of a tree for a given measurement is indicated by a "+" in the appropriate column. (TMP = *Pinus pungens*, VA = *P. virginiana*, P = *P. rigida*, BO = *Quercus velutina*, SCO = *Q. coccinea*, CHO = *Q. prinus*, H = *Tsuga caroliniana*).

STATION	APPROX. ELEVATION IN FT. (m)	SPECIES	TREE #	APPROX. HEIGHT (ft)	DBH (in)	TWIGS 1966	TWIGS 1967	LEADER 1966	LEADER 1967	NEEDLE 1967
OFFICE	1500	TMP	1		1.8	+	*			+
	(457)		2		2.0	+	+			+
		VA	1		1.5	+	+			+
			2		2.0	+				+
			2a		1.8		+			
		BO	1		1.6	+	+			
		SCO	1		2.1	+	+			
		P	1		1.9	+	+			+
		VA	3		2.0	+	+			+
		TMP	3	5		+	+	+	+	+
		VA	4	5 1/2		+	+	+	+	+
		P	2	4		+	+	+	+a	
		TMP	4	7		+	+	+	+a	
		VA	5	6		+	+	+	+	+
		TMP	5	9		+	+	+	+a	
		VA	6	9		+	+	+	+a	

Table 23 (continued)

STATION	APPROX. ELEVATION IN FT. (m)	SPECIES	TREE #	APPROX. HEIGHT (ft)	DBH (in)	TWIGS 1966	TWIGS 1967	LEADER 1966	LEADER 1967	NEEDLE 1967
LOWER POINT,	2200	TMP	1		3.2	+	+			+
MOORE'S KNOB	(671)		2		4.7	+	+			+
		P	1		3.5	+	+			+
			2		4.3	+	+			+
		H	1		2.8	+	+			
UPPER POINT,	2300	TMP	1	8 1/2		+		+		
MOORE'S KNOB	(702)	H	1	5 1/2		+		+		
		TMP	2		7.9	+				
		H	2		5.3	+				
TOP, MOORE'S	2500	TMP	1		12.8	+	*			+
KNOB	(762)		2		8.3	+	+			+
		VA	1		3.7	+	+			+
			2		7.3	+	+			+
		P	1		6.5	+	+			+
		H	1		7.2	+	+			
			2		11.5		+			
		CHO	1		15.3	+	+			
			2		5.1		+			

* insufficient growth on all branches
a cut about July 1, 1967. Current twig length used as 100% in analysis.

desired, cumulative elongation or elongation during a given period was expressed as a percent of total February-August elongation. Tree means of both cumulative and periodic elongation were plotted over time. The 1966 record is a month shorter than for 1967, but still includes most of the growth for most trees except Tsuga caroliniana and Pinus rigida.

Using the growth-per-period plots, times of maximum elongation were compared. All possible comparisons between Table Mountain pine and individuals of a given size (trees were grouped as seedlings or saplings within the "office" site) were made within a given site. Pinus pungens had its maximum two-week elongation earlier than P. virginiana in 5 of 16 comparisons in 1966, and earlier in 5 of 14 in 1967. Pinus pungens was earlier than P. rigida in 4 of 11 comparisons in 1966 and in 4 of 9 in 1967. It was later than these species in no case. Oaks were later than pine in 2 of 6 comparisons in 1966 and in 2 of 4 in 1967. One 1967 comparison had oak earlier than P. pungens. Carolina hemlock growth peaked later than all other trees, 6 to 8 weeks after P. pungens. It also had a qualitatively different growth pattern than the pines. Pine twigs elongate almost completely before the needles begin to expand rapidly, but hemlock needles are almost full-sized, forming a tuft at the

end of the branch, before the axis to which they are attached elongates.

Using the cumulative growth curves for averages of all twigs on a tree, the dates when lines connecting the observed points crossed the 5%, 50% and 95% growth levels were determined. Ninety-five percent dates were available for only some 1967 trees and none in 1966. A multiple regression technique was used to compare the dates the different species reached a given percent growth in each year, after correcting for the effect of elevation. All possible comparisons were made with Table Mountain pine.

Pinus pungens reached 5% growth significantly before all species measured in 1966 except *P. virginiana*. In 1967, the warmer year, it was ahead of *Tsuga* only. It completed 50% of its twig elongation before all other species in 1966, but only before *Tsuga* in 1967. Analysis of 1967 data further indicated that oaks reached 95% elongation earlier than *P. pungens*, which was no different than the other 3 species. The "growing season" for the middle 90% of twig elongation was longer for Table Mountain pine than for *Tsuga* and oaks, but no different than the other pines.

When differences existed, *Pinus pungens* started elongation earliest, but stopped about the same time. (Date of reaching 95% growth varied more within species than growth

initiation.) It accomplished a majority of its growth earlier in the season than other species, when differences between species were present. Individual oaks started late and rapidly completed their growth, as Mowbray (1967) found. *Tsuga caroliniana* started very late, but grew as late as the other conifers in 1967, the only year for which any 95% data were available.

Height Growth of Seedlings

Height growth was measured only on three *Pinus pungens*, a *P. rigida*, and three *P. virginiana* seedlings at the "office" site, and on a Carolina hemlock and Table Mountain pine at the "upper point" site. The growth of the leader lags behind that of the lateral branches. In many cases the maximum growth rate occurred in the two-week period following that for the lateral branches, especially in 1967. The one hemlock measured reached 5% leader elongation a month after the nearby Table Mountain pine. In 1966, two of three *P. pungens* seedlings reached 5% growth before all Virginia pines and the pitch pine. All *P. pungens* leaders did 50% of their growth before other species, by 3 to 22 days. In 1967, a similar situation existed early with the

same P. pungens seedling being slow. P. pungens reached 50% and 95% elongation about 3 days (average) before P. virginiana and 1 to 4 weeks before P. rigida. It thus appears that Table Mountain pine seedlings may make their height growth earlier in the season than the associated pines, although the sample measured was very small.

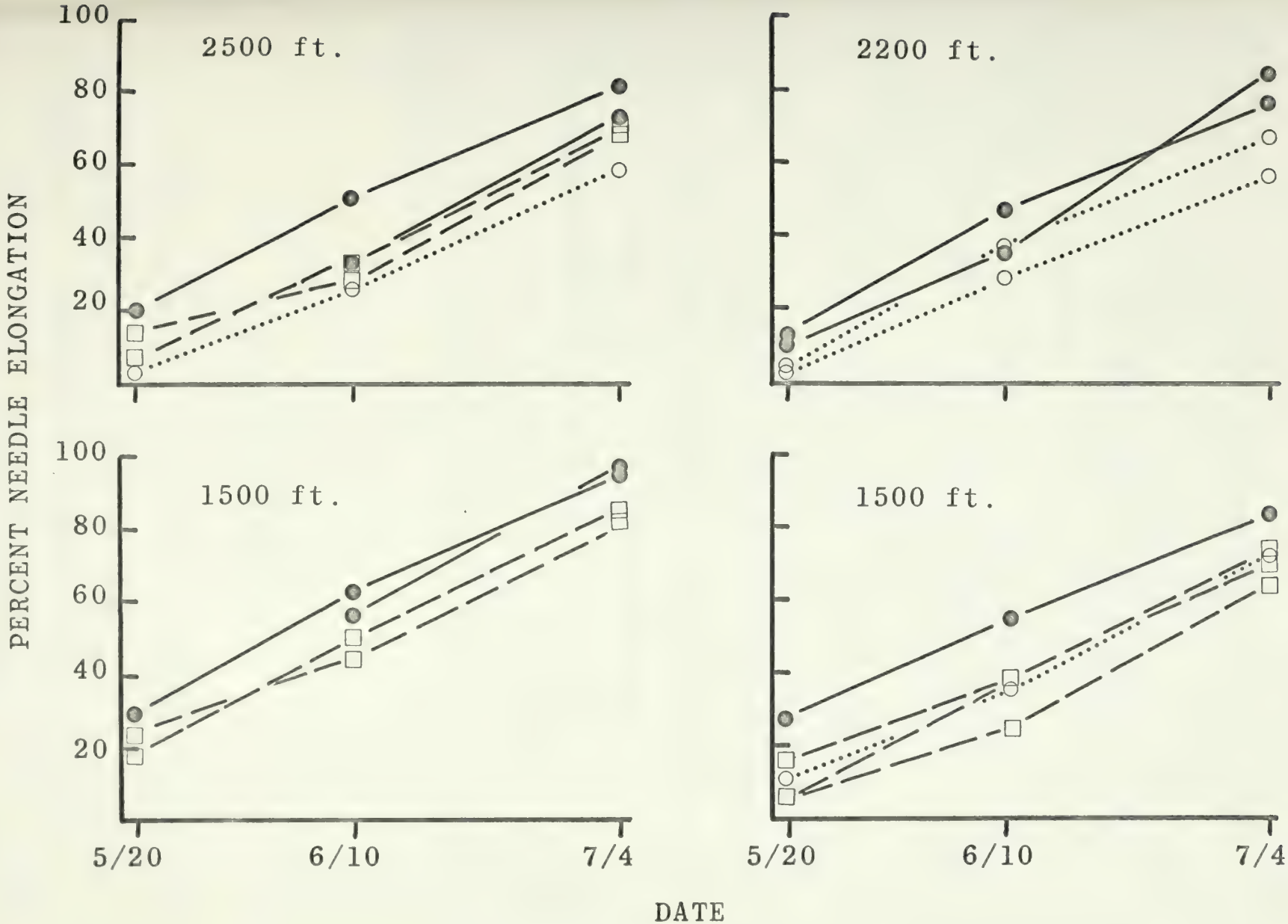
Needle Elongation

Needle elongation was followed only in 1967. Length of one needle at the tip of each of two branches per tree was measured on May 20, June 10, July 4, and August 2. Needle length on the tip of a given branch was fairly uniform. The growth pattern is shown in Fig. 17. In all cases except one (May 20 at the top station), where one species could be said to be ahead of another, Pinus pungens had completed the largest percentage of needle expansion.

Lateral Growth of the Trunk

After some evidence of species differences in timing of twig growth was found in 1966, a few trees were fitted with stainless steel dendrometer bands made as described by

Figure 17. Needle elongation at Hanging Rock State Park, N.C., as a percent of length on August 2, 1967. Each line is the average for a single tree. —— ● *P. pungens*, — — □ *P. virginiana*, ····· ○ *P. rigida*.


2500 ft.
2200 ft.
1500 ft.
1500 ft.
PERCENT NEEDLE ELONGATION
100
80
60
40
20
5/20
6/10
7/4
DATE

Liming (1957), to see if similar differences might exist in lateral stem growth. Larger trees used in the twig studies were banded and a few other trees at the two lower stations were used. In addition, two trees low on Moore's Knob, at 1965 sample area 2, were banded. Trees used in the analysis are listed in Table 24, with dates on which they reached 50% and 90% of their circumferential increase.

Regression analysis showed the 50% growth date to be significantly later at higher elevations, and the period from 50 to 90% growth to be shorter. The date of 90% growth showed no elevational differences. No species differences were found, possibly due to the small sample size. *Pinus pungens* seemed to be somewhat ahead early in the season and then to slow down in midsummer more than the other species. Its growth rate increased somewhat from mid-August through September.

Time of Pollen Release

There is some information on the relative "flowering" dates of *Pinus pungens* and associated pines. In cultivation at Placerville, California, *P. pungens* "flowers" on April 10, on the average, while *P. rigida*, *P. virginiana*, and *P. echinata*

Table 24

Characteristics and dates for 50% and 90% growth of trees used to determine patterns of circumferential increase, Hanging Rock State Park, N.C., 1967. (TMP = *Pinus pungens*, VA = *P. virginiana*, P = *P. rigida*, CHO = *Quercus prinus*, H = *Tsuga caroliniana*).

STATION	ELEVATION FT. (m)	SPECIES	TREE #	DBH (in)	# RINGS AT 4-1/2 FT.	DATE FOR 50% GROWTH	DATE FOR 90% GROWTH
OFFICE	1500	TMP	D1	6.8	36	5/22	8/31
	(457)		D3	5.1	27	6/4	9/19
			D6	14.1	87	5/18	9/2
		VA	D2	5.1	24	6/22	9/10
		P	D5	11.1	73	5/15	10/14
SITE 2	1800	TMP	X1	12.9	97	5/22	7/24
	(548)	VA	X2	15.1	94	6/10	10/15
LOWER POINT	2200	TMP	TMP2	4.7	22	5/28	9/20
	(671)		D8	11.2	110	6/8	9/21
		P	P2	4.3	28	6/1	7/10
			D7	11.1	107	5/24	9/2
		H	D9	7.2	52	6/11	8/24
TOP	2500	TMP	TMP1	12.8	80	6/10	9/12
	(702)		TMP2	8.3	69	6/17	9/15
		VA	VA2	7.3	28	6/28	8/31
		P	P1	6.5	83	7/13	9/24
		H	H1	7.2	89	6/1	7/14
		CHO	CHO2	5.1	43	5/8	8/10

"flower" on April 21 and 23, and May 1, respectively (Liddicoet & Righter, 1960). In 1954, at 2300 feet (702 m) in Buncombe County, North Carolina, Table Mountain pine started to shed pollen 3 weeks before pitch and Virginia pines, and 4 weeks before shortleaf pine. It finished shedding 9 days before any other species began (Dorman & Barber, 1956). To investigate this further, time of pollen release for three pine species was recorded whenever it was observed. Table 25 lists the areas and dates of observations and the condition of the species with respect to pollen release.

In all cases where species could be compared, P. pungens released its pollen earlier than associated pine species, with P. virginiana second. The interval between maximum shed of Table Mountain and Virginia pines appeared to be just over two weeks at 1500 feet in Hanging Rock State Park, and somewhat less at 2500 feet. P. rigida was a week or two later than P. virginiana. Sequences were similar at two spots in Virginia. There is a two-week lag between 1500 and 2500 feet for P. pungens, and slightly less for P. virginiana. A similar difference was found between years, with earlier pollen release during the warmer year (Fig. 18e). Although Table Mountain pine released its pollen earlier than other pine species, slight amounts remained in the strobili when pollination of P. virginiana occurred, in some

Table 25

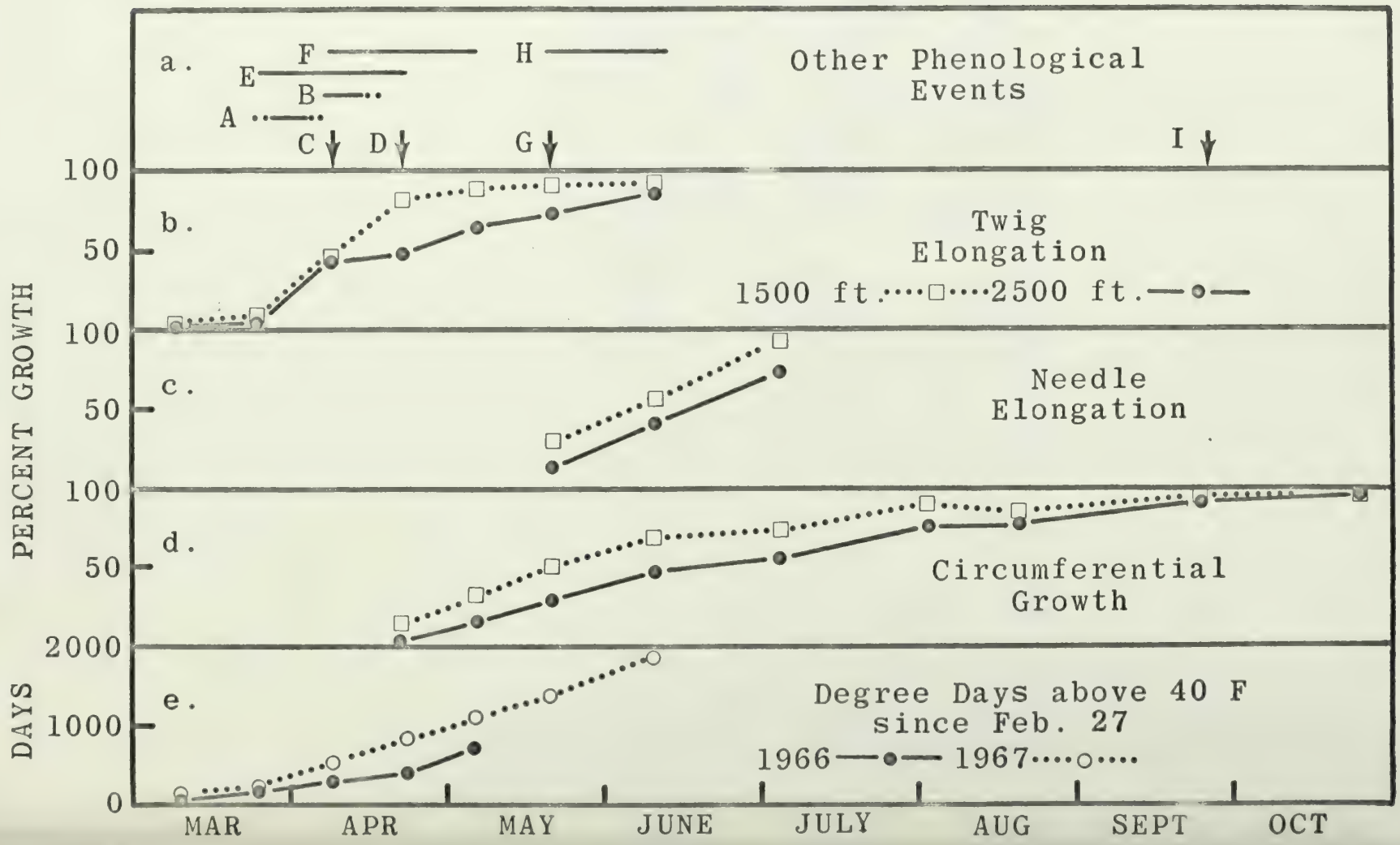
Observations of time of pollen release of Table Mountain pine and associated pines.

LOCATION	APPROX. ELEVATION FT. (m)	DATE	CONDITION OF POLLEN RELEASE		
			P. pungens	*P. virginiana*	*P. rigida*
Hanging Rock State Park, N.C.	1500 (457)	4/22/66	Just over	Not begun	Not begun
		5/8/66	----	Completed	Just over
		4/8/67	Completed	Beginning	Not begun
		4/22/67	----	Completed	?
	1700 (508)	5/8/66			Maximum
		4/8/67	Mostly completed	Just beginning	Not begun
		4/22/67	Completed	Completed	Maximum
	2200 (671)	4/22/66	Beginning	-----	Not begun
		5/8/66	Completed	-----	Just beginning
		4/8/67	Maximum to over	-----	Not begun
		4/22/67	Completed	-----	Not begun
	2400 (732)	5/8/66	Just completed	-----	-----
	2500 (762)	4/22/66	Not begun	Not begun	Not begun
		5/8/66	Completed	In progress	Not begun

Table 25 (continued)

LOCATION	APPROX. ELEVATION FT. (m)	DATE	CONDITION OF POLLEN RELEASE		
			P. pungens	*P. virginiana*	*P. rigida*
		4/8/67	Just beginning	Not begun	Not begun
		4/22/67	Completed	In progress	Not begun
Rocky Face, Alexander Co., N.C.	1800 (548)	4/11/66	Just beginning	-----	-----
Smith Mtn., Pittsylvania Co., Va.	1300-1500 (396-457)	5/1/66	Over	Just beginning	Not begun
Near Reddish Knob, Augusta Co., Va.	3500 (1067)	5/8/65	In progress	-----	-----
	3900 (1279)	5/8/65	In progress	-----	Not begun

Figure 18. Phenology of Pinus pungens at 1500 and 2500 feet, Hanging Rock State Park, N.C., 1967, compared with that of some associated species. Degree days above 40 F at 1500 feet are also shown for 1966 and 1967. a) A = pollen release, Pinus pungens, 1500 ft. B = pollen release, P. pungens, 2500 ft. C = Amelanchier sp. and Leucothoe recurva in flower; Quercus, Betula, Amelanchier, Vaccinium buds breaking, 2500 ft. D = P. virginiana, Quercus, Vaccinium, Gaylussacia in flower, 2500 ft. E = Oak twigs elongate, 1500 ft. F = Oak twigs elongate, 2500 ft. G = Oak leaves mature; Rhododendron catawbiense, Kalmia latifolia starting to flower, 2500 ft. H = Hemlock twigs elongate. I = Q. prinus acorns fall. b) Twig elongation, Pinus pungens, percent of length on Aug. 2. c) Needle elongation, Pinus pungens, percent of length on Aug. 2. d) Circumferential increase, percent of total by Dec. 9. e) Degree days above 40 F at 1500 ft. since Feb. 27.


a.
F
H
E
B
A
C
D
G
I
Other Phenological Events
b.
Twig Elongation
1500 ft.
2500 ft.
c.
Needle Elongation
d.
Circumferential Growth
e.
Degree Days above 40 F since Feb. 27
1966
1967
PERCENT GROWTH
DAYS
100
50
2000
1000
0
MAR
APR
MAY
JUNE
JULY
AUG
SEPT
OCT

cases.

Discussion

The relationship between various growth processes of Pinus pungens at 1500 and 2500 feet (457 and 762 m) in Hanging Rock State Park is shown in Fig. 18, and related to other phenological events at the sites.

Both twig elongation and pollen release were earlier in 1967 than in 1966. The only weather records available for the park are maximum and minimum temperatures taken at the park office near the 1500 foot station. Although the temperatures were measured under the shelter of a porch roof and were not indicative of those in the field, especially at higher elevations, they should indicate the pattern and magnitude of differences between 1966 and 1967. For each year, degree-days above 40 F (4.4 C) were calculated for the period between each set of measurements, as degree-days = (average daily mean temperature for the period -40) X (number of days in the period). These are plotted in Fig. 18e. 1967 was warmer in late February and early March, and especially in late March through mid-April, but was cooler in late April and early May. The differences between "flowering" dates and

dates for reaching 50% twig elongation in 1966 and 1967 averaged about the same as the time difference between the cumulative degree-day curves during the same time period. Pinus pungens was somewhat less different between years. It reached 50% elongation an average of 8.4 days earlier in 1967, but the other pines were 14 days earlier.

U. S. Weather Bureau data indicates that late winter and early spring of 1966 in the northern North Carolina piedmont was considerably colder than the average year, and that 1967 was somewhat warmer. Mean monthly temperature differences (1967-1966) for January through April at Danbury, at 800 feet, 4 miles east of the park office were +7.9 F, -1.2 F, +3.5 F and +5.9 F. Precipitation in 1966 exceeded that in 1967, except in March. It was below normal both years except in January and February, 1966. Data for May, 1966, are not available for Danbury because the weather station moved during 1966. The general relationship between the years was the same for the region as a whole, although the difference between years at Danbury may include an unknown location factor.

It appears that growth and reproductive activities of Table Mountain pine occur as early or earlier than those of associated species. Advantages to Pinus pungens from this situation might include growing while vapor pressure

deficit is low and while there is minimal competition for water, light, and nutrients from its less active and, in some cases, leafless competitors. It would also allow the maximum time for photosynthesis by new foliage (and by the young green twigs), which was the most efficient for several pines studied by Freeland (1952). Where late frosts are likely, however, this early activity of Pinus pungens would expose the young growth and developing reproductive portions of the tree to frost damage more often than if it were to develop later. Conceivably, frequent late frosts could exclude the species from these areas by limiting growth and reproduction. Frost damage to female strobili of Pinus echinata occurred only on those which were not covered by bud scales (Campbell, 1955). Freezing weather caused greater damage to emerging conelets of P. attenuata than to those further developed (Krugman, 1966). A small difference in stage of development apparently makes a large difference in susceptibility to damage.

Weather may also affect reproduction in other ways. Freezing during meiosis can cause pollen inviability. The response of rate of development of the male and female strobili to temperature is different, and unusual weather may cause pine pollen "flight" and female receptivity to be out of phase (B. J. Zobel, personal communication). If early

reproductive activity is a trait the species retains throughout its range, this alone could exclude the pine from extensively colonizing areas with later spring frosts, and might help explain northern and northwestern range limits and "blank spots" in its distribution.

Two areas in the North Carolina mountains where Pinus pungens appears to be quite rare, if present at all, are in eastern Alleghany and central Ashe Counties, southwest through Watauga, Avery and Mitchell Counties, and in the whole interior of western North Carolina west of Transylvania, Buncombe, and Yancey Counties. These areas coincide with areas in the state where late spring frosts are most likely (Hardy, 1964). The species is also quite rare west of the Alleghany Front in West Virginia, where temperatures average 6-7 F (3.3-3.9 C) lower, and growing seasons are shorter, than in the Valley-and-Ridge province (Clarkson, 1966). A similar situation occurs in Pennsylvania, where the species has not been reported from west or north of the Appalachian Plateau front. Its northern limit of distribution generally coincides with the location of a greatly steepened temperature gradient which occurs south of the Plateau front. This gradient is most evident in mean January minimum and maximum temperatures and in mean maximum temperature in July (U. S.

Dep. Commerce, 1960).

Critchfield (1963) suggested, on the basis of pollen release dates from Dorman & Barber (1956), that *P. pungens* might be reproductively isolated from the species with which it occurs. Partial isolation by 2 week to 4 week average differences in time of pollen release is also suggested for other pine species, between which limited hybridization occurs (Critchfield, 1963; Haller, 1962; Little *et al.*, 1967).

VII. SEED GERMINATION STUDIES

The absence of *Pinus pungens* from some types of topography could be partially due to an effect on the establishment of seedlings. Since large soil temperature differences exist between aspects in the spring (Geiger, 1965), the effect of temperature on seed germination was investigated. In a preliminary experiment, a few soaked seeds of *Pinus pungens* from several areas, and of *P. rigida* and *P. virginiana* from two areas, were planted in a flat of sand. The flat was placed in a controlled temperature box with a 12-hour photoperiod and thermoperiod (55 F, 35 F) (12.8, 1.7 C), on February 3, 1967. On April 15, the flat was moved to the greenhouse. At this time, 3 of 58 *P. pungens* seeds had germinated, while 16 of 35 of the other species germinated. After 11 days in the greenhouse, 54 of the remaining 55 *P. pungens* and 16 of 19 remaining of the other species germinated. A need for stratification of Table Mountain pine seed could cause such an inhibition of germination.

However, since seed from the sources used had germinated easily in the greenhouse in previous experiments, a differential response of the species to temperature was hypothesized, and the effect of temperature on germination was investigated more closely.

Temperature-gradient Bar: Methods

The temperature-gradient bar and chamber described by Barbour & Racine (1967) were used for germination studies. Temperatures of the baths which heated and cooled opposite ends of the bar were checked at least daily. Bar temperatures were measured with thermocouples at 11 of 21 "stations" on the bar, for three hot-bath temperatures. Average bar temperatures used in the analyses were determined by linear interpolation using the known bath-temperature to bar-temperature relationships. Seeds were soaked in distilled water overnight at 36 F and dipped in a slurry of "Semesan" fungicide before the experiment started. They were germinated on sand in plastic petri plates 5 cm in diameter, placed at either 11 odd-numbered or 10 even-numbered stations. Twenty (in experiment G4) or 25 seeds per plate were used. Two or three seed sources could be

used in one experiment. As necessary, water was added to plates on the hot end and removed from those on the cold end of the bar. Cumulative seed germination was determined twice a day for seven days and once a day through the twentieth day, when the experiments were terminated. Seeds were removed from the dishes after seedling root elongation was well started. "Germination" was defined as the protrusion of the tip of the radicle past the tip of the split seed coat. This proved to be a poor definition, as some hotter treatments just "germinated" and developed no further. In experiments G5 to G8, the number of "germinated" seeds was reduced by the number which failed to elongate further, before the data were analyzed. In correcting, it was assumed that unelongated seeds were the last to germinate, giving the maximum average speed of germination to those which did elongate. Thus, speed of germination for temperatures where non-elongation was most prevalent, above about 28 C, was probably overestimated. Although seed lots were cleaned before use to eliminate hollow seeds, ungerminated seed was checked and germination percentages adjusted to exclude hollow seeds which had been used (less than 1% of the total).

Germination data were expressed by the "Germination Value" (GV) of Czabator (1962). This index combines measures

of the total germination (Mean Daily Germination or "MDG") and the maximum average daily rate of germination obtained during the experiment (Peak Value or "PV"). GV equals the product of MDG and PV. Since the interest here was to determine at what temperature a source or species had maximal GV, rather than which source would have maximum GV at a given temperature, a Relative Germination Value or "RGV" was calculated by dividing GV at a temperature by the maximum GV found for the source in the experiment. This made comparison of response to temperature by different seed lots much easier. RGV, MDG, and PV were plotted over station temperature for all experiments.

Experiments were designed to determine differences between species of pines from a given source and between different sources of *Pinus pungens*.

Preliminary Experiments

Experiment G1. Seeds from one tree each of three species from 1965 sample area 4 were used. This experiment indicated that good germination and a wide range of germination values could be obtained with the experimental conditions used, and that 20 days would include most germination. During the 20-27 day period, only 4 seeds germinated, compared to 506

in the first 20 days.

Experiments G2 and G3. Sample area 19 *Pinus pungens* seed germinated very poorly in a comparison with area 12 at three low and two high temperatures (Experiment G2). In Experiment G3, seeds from areas 12 and 19 were stratified for 17 days at 34 F. Maximum GV for stratified seed was 5.0 and 0.0 for the two areas, compared with 143 and 35 in Experiment 2, indicating a possible adverse effect of stratification on germination.

Experiments G4 and G6: Species Comparisons

Comparisons between *Pinus pungens*, *P. virginiana* and *P. rigida* were made for seed from sample area 4, at 3200 feet (947 m) on the Blue Ridge in Patrick County, Virginia, and from 1500-1900 feet (457-580 m) on Smith Mountain, Pittsylvania County, Virginia, an outlying monadnock about 45 miles (72 km) east-northeast of area 4. For each area, seed from two to five trees of each species, depending on what was available, was mixed, with equal numbers from each tree of a species at each temperature. RGV's for the three species from Smith Mountain are shown in Fig. 19a, and MDG and PV in Fig. 20a. (These data are not corrected for "germinated" seeds which did not elongate.) RGV for all species rapidly increases

above 17 C, with Pinus pungens increasing most rapidly at first, until all species reach a maximum about 26 C and then drop rapidly above 30 to 32 C. Some irregularity in the curves appears at 28 to 31 C in several experiments and is perhaps due to internal pathogenic fungi (Fisher, 1941) which have temperature optima in this range.

The relationship of RGV curves might be expected on the basis of species distributions around Smith Mountain. Table Mountain pine is rare below about 1400 feet. P. rigida is at all elevations on the mountain and quite common on the surrounding Piedmont. P. virginiana, the most common pine on the Piedmont, is rare above about 1500 feet.

In Experiment G6, using seed from area 4, data corrected for non-elongation resulted in the RGV, PV, and MDG curves in Fig. 19b and 20b. Pinus pungens again is somewhat ahead of the other species below 26 C, reaching a peak at 23 C, while P. virginiana and P. rigida peak at 30 and 28 C, respectively. Again P. pungens seems better adapted to relatively lower temperatures. P. rigida seems to germinate to a significant degree over a wider range of temperatures than the other species.

For both areas, P. rigida has the maximum GV, with P. pungens well below the other two species. This is due to a higher maximum PV for P. rigida and to the fact that maximum

PV and MDG occur at the same temperature, while for Table Mountain pine, PV peaks at temperatures above those for maximum MDG.

Experiments G5, G7, and G8: Comparison of *Pinus pungens* from Different Sources

Two Blue Ridge:Valley-and-Ridge comparisons were made in Experiments G5 and G7. RGV's are plotted in Fig. 19c, and MDG and PV are in Fig. 21a. In Experiment G5, sample area 4 was compared with seed from Iron Mountain, Smyth County, Virginia, about 8 miles south-southeast of Marion, at 3200 feet. Site 4 *Pinus pungens* seed again showed the dip in germination about 29 C. Despite this aberration, the RGV curve for site 4 is slightly shifted toward warmer temperatures. Maximum GV for the two sites was almost the same.

Experiment G7 compared seed from four trees each at area L (including 1965 area 6) and area 16. Maximum GV was 116 for area L and 42 for area 16. The low GV for area 16 seed was due to poor germination, which never exceeded 64%, as well as slow germination.

Experiment G8 used seed from areas N, F, and B, at latitudes 34°39', 38°17', and 39°49' N. Seeds from three, five and two trees were available, respectively, from the

Figure 19. Relative germination values (RGV) on temperature-gradient bar. a) Expt. G4, 3 species from Smith Mountain. b) Expt. G6, 3 species from area 4. c) *Pinus pungens*, from areas 4 and L on the Blue Ridge, and from area 16 and Smyth Co., Va., in the Valley-and-Ridge. d) *P. pungens* from areas N, F and B.

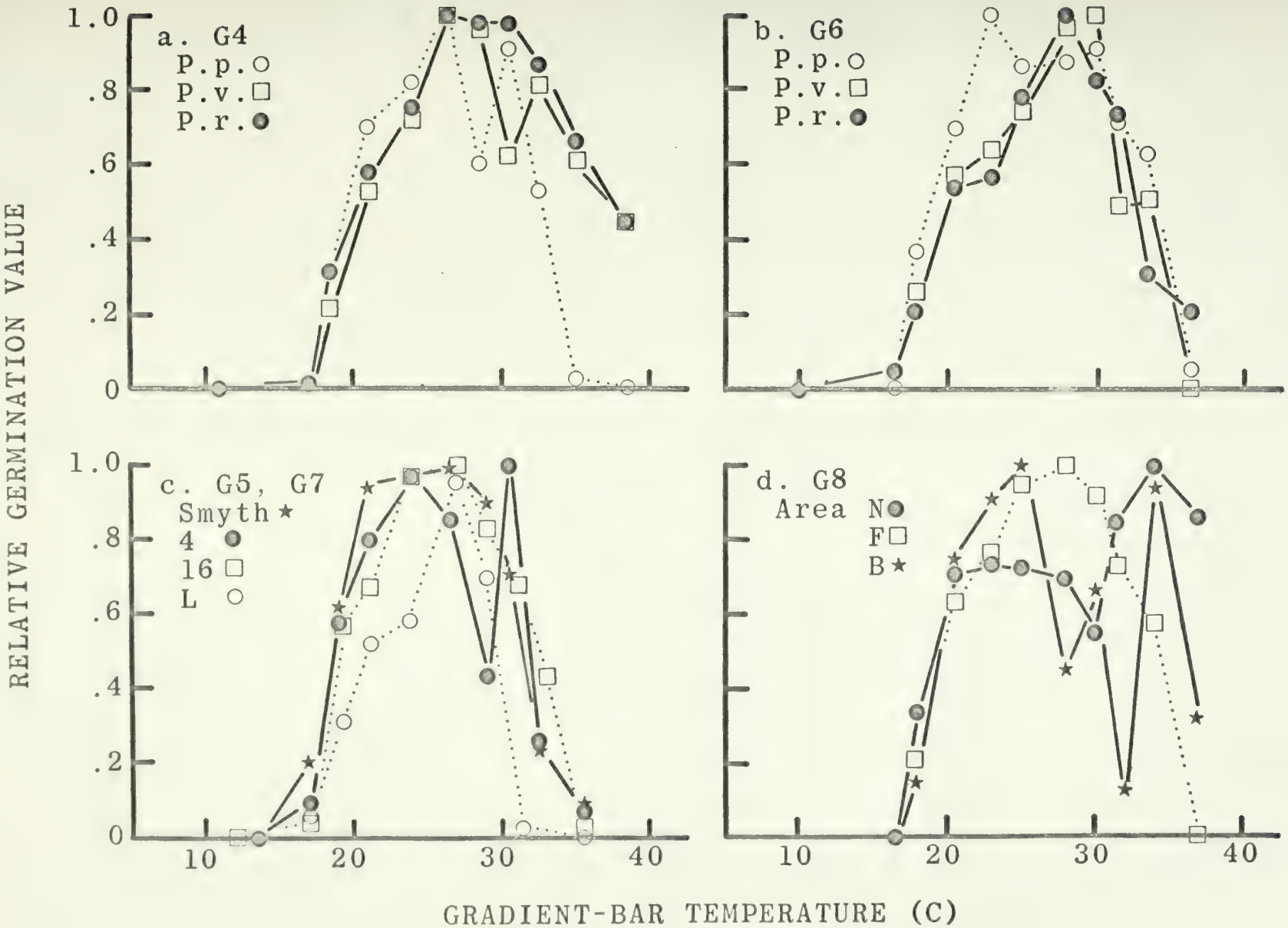

a. G4
P.p.
P.v.
P.r.
b. G6
P.p.
P.v.
P.r.
c. G5, G7
Smyth
4
16
L
d. G8
Area N
F
B
RELATIVE GERMINATION VALUE
1.0
.8
.6
.4
.2
0
10
20
30
40
GRADIENT-BAR TEMPERATURE (C)

Figure 20. Peak Value and Mean Daily Germination for species comparisons: a) Expt. G4, Smith Mountain, Virginia. b) Expt. G6, area 4.

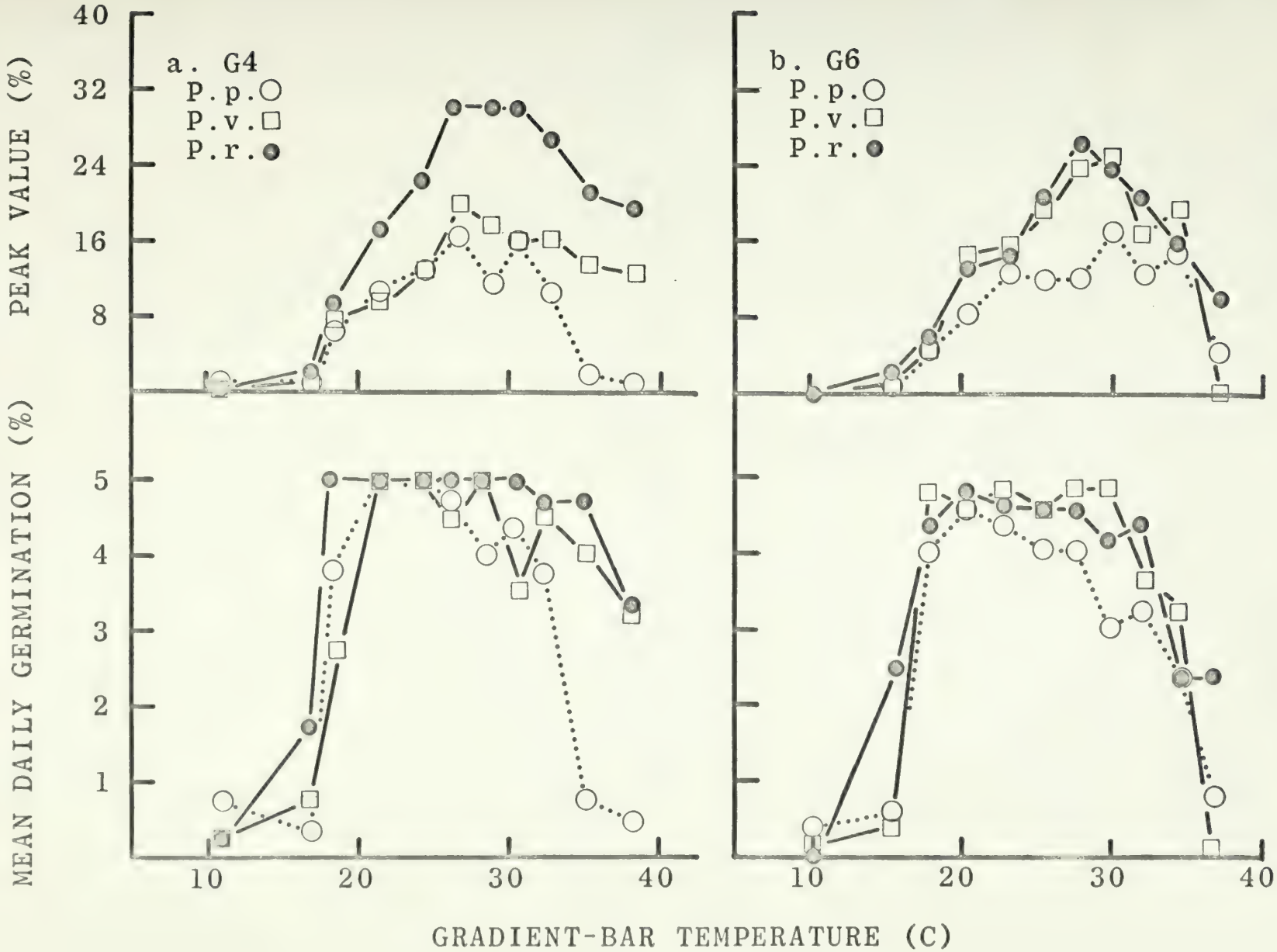
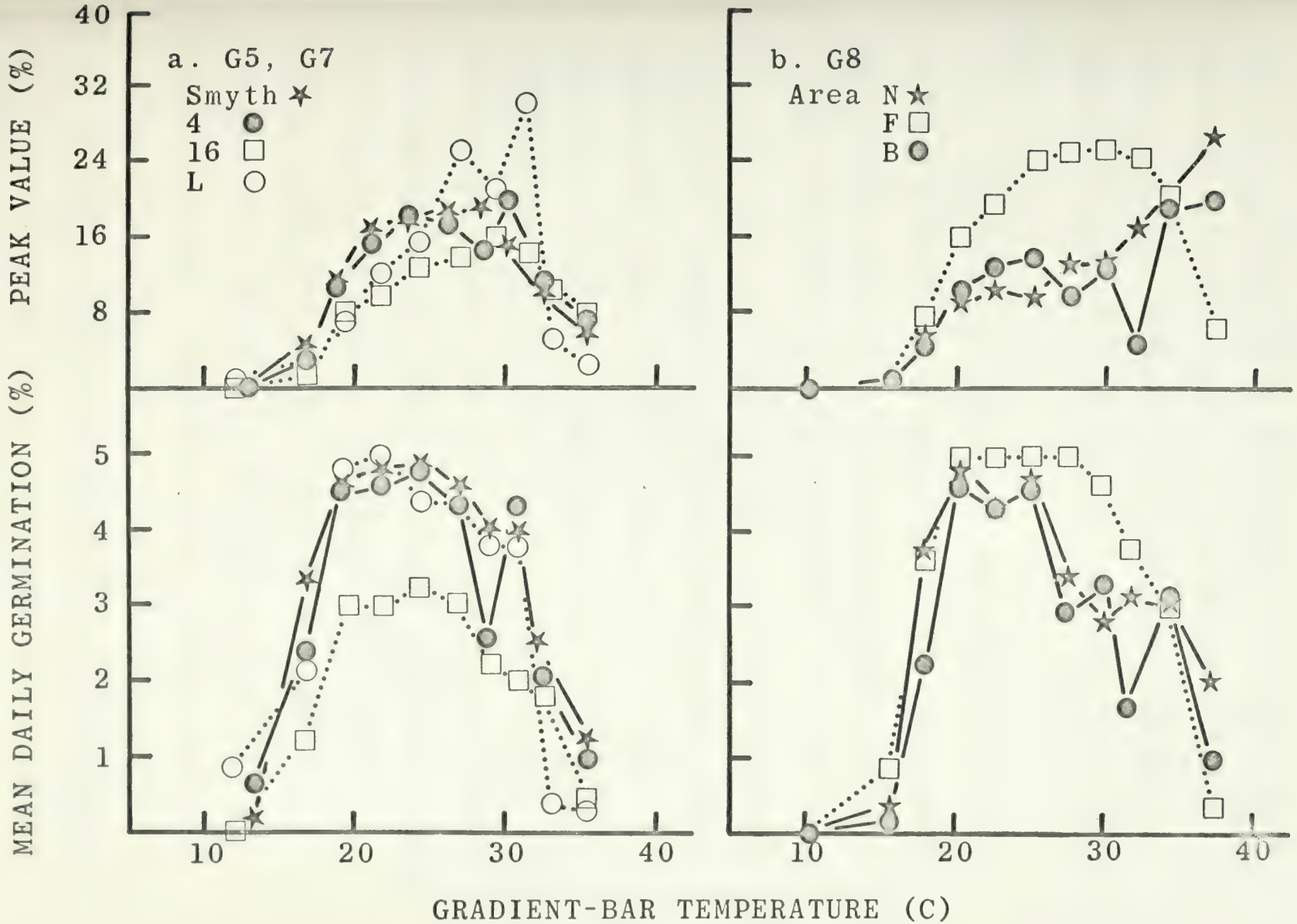

a. G4
P.p.
P.v.
P.r.
b. G6
P.p.
P.v.
P.r.
PEAK VALUE (%)
MEAN DAILY GERMINATION (%)
40
32
24
16
8
5
4
3
2
1
10
20
30
40
GRADIENT-BAR TEMPERATURE (C)

Figure 21. Peak Value and Mean Daily Germination for comparison of sources of *Pinus pungens*: a) Expt. G5 and G7, Blue Ridge:Valley-and-Ridge. b) Expt. G8, latitudinal comparison.


a. G5, G7
Smyth
4
16
L
b. G8
Area N
F
B
PEAK VALUE (%)
MEAN DAILY GERMINATION (%)
40
32
24
16
8
5
4
3
2
1
10
20
30
40
GRADIENT-BAR TEMPERATURE (C)

three sources. RGV curves for areas B and N (Fig. 19d) were very erratic in the 28 to 31 C temperature range, making comparison of the results difficult. MDG and PV are plotted in Fig. 21b. Maximum GV was 85 for B, 62 for N, and 125 for F.

Despite the aberrations in the data apparently caused by internal fungal infection of some seed samples, some idea of variation in seed germination patterns may be obtained from the data presented here. It appeared that seed tested from the Ridge-and-Valley area had a somewhat lower optimum temperature than that from the Blue Ridge, even when the Ridge-and-Valley source is at a lower elevation than the Blue Ridge source. The latitudinal comparison was badly distorted and also included a large elevational difference, with areas B and N about 1200 to 1300 feet and F above 2900 feet. Seeds from the two lower sites appeared to be better adapted to the highest temperatures used than those from site F. Optimal temperature for RGV for N, the southern source, appeared higher than for F. One cannot guess at what temperature the true maximum RGV for area B appeared.

In the field, the important part of the temperature response of seeds should be at the lower temperatures. Seeds which germinate in early spring will respond as soon

as possible, not waiting for "optimum" temperatures. Total germination for Table Mountain pine seeds (represented by MDG) was maximal at temperatures below those at which maximal speed of germination (represented by PV) occurred. The relatively high temperature maximum of PV could be important for *Pinus pungens* if the seeds were released by a warm season fire, when it would be necessary to complete the germination process rapidly to insure establishment before desiccation killed the young seedlings. The three species show some difference in this respect. *Pinus rigida* and *P. virginiana*, which release their seeds the fall or winter after they mature, and, thus, would almost always germinate in the spring, show no separation or less separation of temperatures at which maximum survival and speed of germination occur. Usually, these two species had maximum speed of germination at the upper end of the maximum-survival temperature range, which extends to somewhat higher temperatures than for *P. pungens*.

Germination in the above experiments was at constant temperature in continually wet conditions, and probably at a different pH than would be found under natural conditions. It may be that the temperature responses outlined above would not occur under different conditions, such as alternating day-night temperatures. Some indication of such

differences appears in germination records kept for greenhouse experiments. Seeds were planted in small pots in soil from sample area I. Time to germination varied considerably, depending on conditions of germination, with a median of about 10 to about 20 days from planting of soaked seed to emergence of the seedling. Pinus rigida, which had the highest PV in the gradient-bar experiments, was the slowest to germinate in 3 of 4 large greenhouse plantings.

Seed of Pinus contorta from British Columbia showed a pattern of germination depending on its source. Seed from colder areas germinated more quickly at low temperatures than that from warmer areas. Those seeds from warmer areas germinated more quickly at high temperatures than those from cooler areas (Haasis & Thrupp, 1931). Critchfield (1957) found no differences he could correlate directly with climate, but said his pretreatment of the seed might be responsible for eliminating such a response. He did find definite differences between seed from various regions, however.

Seeds of all species used in these experiments germinated well, in most cases. In one experiment with area I soil, 95%, 93% and 88% of solid Pinus pungens, P. rigida and P. virginiana seed germinated. Maull (1963) found decreases in germination of Pinus rigida seed with decreasing soil moisture, with periods of wetting and drying, and in

the light. No change by pH from 4.5 to 8.3 was found. However, some soils used in the present greenhouse experiments had pH below 4.5. Although germination percentages were not determined for all plantings, germination of solid seed was in the 80-90% range most of the time. Exceptions were usually those lots collected in early fall of the year they matured, probably before the cones were fully ripe.

Effective germination in the field is probably much below this. The percentage of empty seeds removed before use of the lots of seed varied from 6 to 73% of the total, in measurements made for 16 trees from areas N, F, and P. The 16 lots averaged 73% full.

VIII. PHYSIOLOGICAL RESPONSE OF SEEDLINGS

In order to understand how some conditions found in the field might limit the range of *Pinus pungens*, some aspects of seedling physiology were investigated.

Water Relations

Differences in resistance to damage by limited soil water may be related to the ability of a plant to avoid water loss, or to endure dehydration of the protoplasm without injury. The former category includes depth and extent of root systems and their ability to function at low soil moisture contents, and the extent of control over water loss by the leaves. Although few trees can endure protoplasmic dehydration to the extent that some lower plants can, differences between species and throughout the year within a species are the ultimate factor determining their drought resistance (Kramer & Kozlowski, 1960). The

adverse effect of water deficits may result from changes in a number of basic cell processes. Net photosynthesis may be affected by stomatal closure, which limits CO_2 entry and raises leaf temperatures, or by direct effects on enzymatic systems in the cells (Slatyer, 1967). Whitmore & Zahner (1967) present evidence that water stress in differentiating xylem cells directly reduces carbohydrate incorporation into the cell wall.

Differences in species characteristics involved in prevention of internal water deficits, and in the response to them, may in large part explain distributional differences between some pine species (Daubenmire, 1943; Rand, 1965; Wright, 1966). Similar differences might affect distributions of the pine species which occur in the Appalachian Mountains. *Pinus pungens* is the most restricted of the species, occupying the warmest and driest topographic situations, which usually have shallow soil. It appears that, relative to the other species available for colonization, *P. pungens* must be better adapted to survival and growth in these habitats where maximal soil water deficits probably exist. Since Table Mountain pine occupies a wide latitudinal and elevational range, any adaptations to drought might exist in different degrees in different populations. To determine the extent of differences, if any, between geographic sources

of P. pungens and between species, some aspects of water relations of seedlings were compared.

Seed was collected during 1965 sampling and the following fall. Sample areas and number of trees of Pinus pungens from which seed was used from each area were as follows: Area 1(2 +1 P. virginiana), area 4 (3 + 1 P. virginiana + 1 P. rigida), area 9 (1),area 26 (1), area 27 (2), collection BB (near Brasstown Bald, Towns County, Georgia, at 2450 feet) (1). Plantings were made in late January of 1966 and 1967. Each planting consisted of twenty pots from each mother tree (four pots each in five replications). Plants were grown in 16-ounce foam plastic cups (Dart no. 16H16). All cups were wrapped with aluminum foil in January, 1967, to discourage algal growth at the surface between the soil and the transluscent cup.

To provide a nutrient and microbiological environment resembling that in natural conditions, soil from sample area 11 (1966 area I) was collected. The topsoil and subsoil which passed through a 1/2-inch seive were mixed. Analysis of 1965 soil samples indicated that this soil approximated average textural and nutrient conditions encountered. The analysis of area 11 soil is shown in Table 26.

Mycorrhizal associations increase mineral absorption of pines by increasing root surface and by accumulating some

Table 26

Characteristics of soil from area I (area 11), used to grow seedlings for experiments D and T. Each value is the mean of 5 determinations.

	Texture				Chemistry						
	>2 mm (Percent of Total)	Sand (% of<2 mm sample)	Silt	Clay	pH	Ca lb/acre	Mg lb/acre	Mn lb/acre	P lb/acre	K lb/acre	OM %
MEAN	41	59	24	17	4.1	172	22	7.6	2.4	78	2.2
STANDARD DEV.	4.1	0.7	0.7	0.5	0.1	16	5	0.8	0.6	0	0.1

nutrients. They protect roots from some pathogens (Marx & Davey, 1967). Other roles may include supplying metabolites or growth substances and increasing drought resistance (Harley, 1965; Mirov, 1967) and perhaps fixing nitrogen (Richards & Voigt, 1964). It was considered desirable to supply conditions under which this important relationship could develop, by providing the organisms and soil nutrient conditions which existed in an area where all the pine species under consideration were present. Development of the seedling presumably depends largely on nutritional conditions, which mycorrhizae influence in pines. Since plants grew in small soil volumes, however, the total pool of nutrients available to them was somewhat limited.

Plants started in January, 1966, were moved outside the greenhouse from late April until January 11, 1967, when they were moved back into the greenhouse. These plants and the duplicate 1967 planting are referred to as the "D" planting.

Experiment D. The relationships of several plant responses to drying were determined in this experiment. Pots were saturated and, about a day later, covered with "Saran-wrap", which was sealed around the seedling stem with tape. Pots were then allowed to dry by transpiration. No plants were used within two days after saturation to

assure drainage of most free water. Two replications (i.e. eight plants of each age from each mother tree) of the "D"-planting were used. Each age was broken into eight groups, each group having one pot from each of the 13 mother trees. Order in which groups, and trees within groups, were used was randomized. Almost all sampling was done about 8 a.m. (daylight time). A shaded Bendix-Friez hygrothermograph, kept with the plants, indicated this to be about the time that relative humidity began to fall from the usual nightly maximum of 100%. Thus, this should have been the time of minimal water stress in the plants, after maximum time for recovery from the water stress developed the previous day (Slatyer, 1967).

Usually, five pots per day were sampled. Each pot was weighed the two days before it was scheduled to be used, and at the time of sampling. The Saran-wrap cover was removed and the pot was placed in an enclosed "moist chamber", where sampling was done. Needles were removed for water potential determinations. Secondary needles were used from the older plants, while the entire top above the cotyledons was used from the younger ones. The soil was then dumped from the pot and the roots removed, and it was thoroughly and rapidly mixed by hand, breaking the large aggregates. A small sample was taken for water potential

determination. A sample of 250 to 300 grams of the remainder was weighed, dried at 105 C for at least 24 hours and re-weighed to determine the bulk soil moisture content. Roots were thoroughly washed, the plant dried at 70 C about 24 hours, and dry weights of needles, stem, and roots determined. After water potential measurements were completed, percent moisture of needle and soil samples used in the measurements were determined by similar weighing and drying. Dry weight of each needle sample was added to total needle weight. For the younger plants, total top weight was not separated into needle and stem.

Water potentials were determined with a thermocouple psychrometer (Richards & Ogata, 1958; Boyer, 1965). Double-thermocouple psychrometers, with one wet and one dry thermocouple junction, were used with needle samples to obtain potentials corrected for respiration heat of the tissue (Barrs, 1965). Needle samples were cut into sections about 1 cm long, covering the bottom of the psychrometer cup. Psychrometers were calibrated with sucrose solutions of known potential placed in the bottom of the cups. The "water potential" terminology of cell-water relations, as outlined by Kramer et al. (1966), is used. Measurements were made from May 3 to June 30, 1967, after all year-old seedlings had elongated and developed new needles.

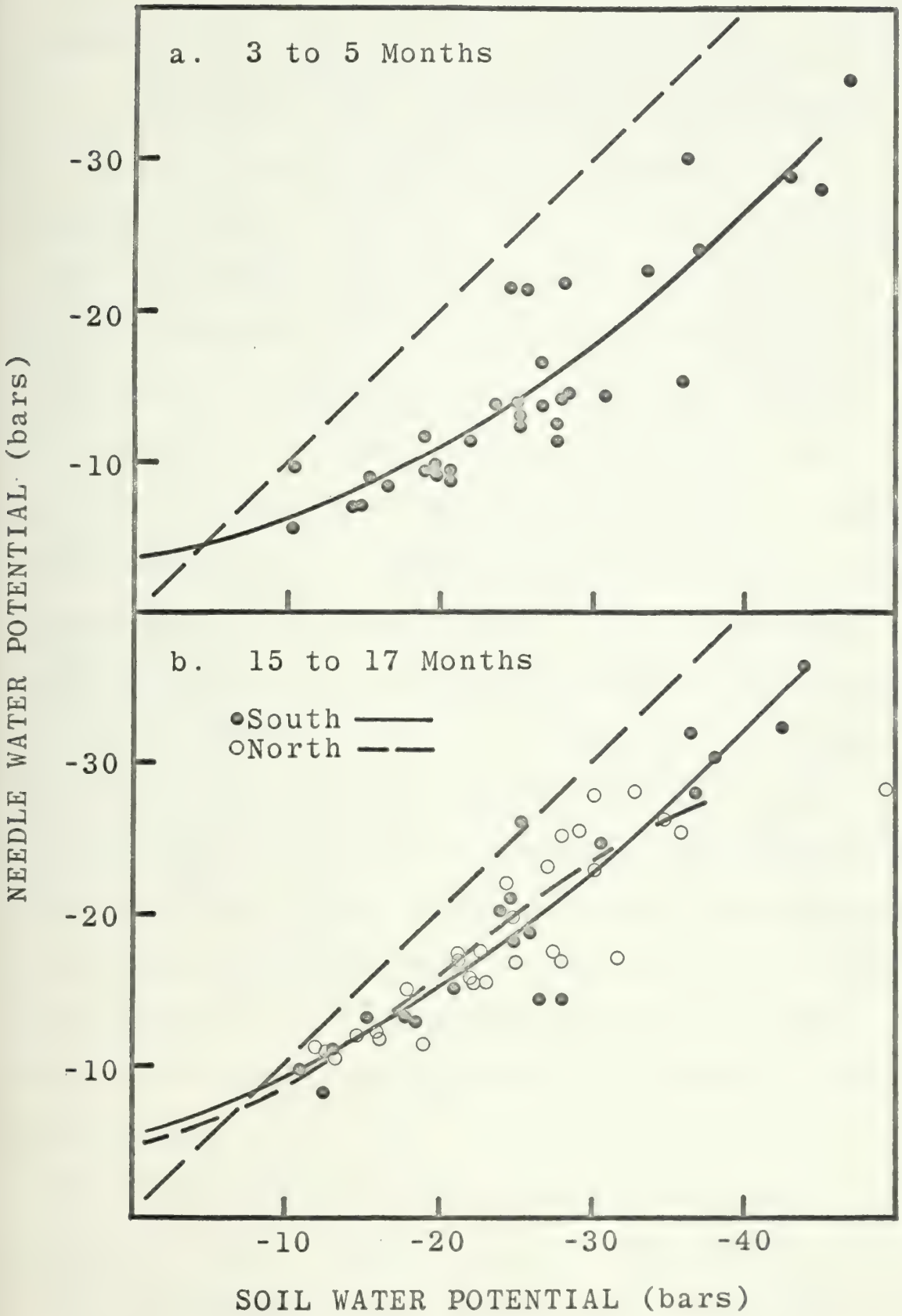
Water content:water potential relationships of the soil. For use in future experiments, a water content:water potential curve was determined for the soil. Relationships were determined using water content of the sample on which the potential was measured and of the bulk sample The regression of water potential of the soil (Ψ_s) on water content of the bulk soil gave the best regression, accounting for 94% of the variation for soils of both older ("O") and younger ("Y") groups of plants. The two regression lines differed somewhat, however.

Soil water potential:needle water potential relationships. Regression equations were calculated for seedlings from each mother tree at each age, and for trees grouped in various ways. The reduction in sum of squares using separate regressions over that using a single pooled regression determined whether regression lines for different groups of seedlings were significantly different. Comparisons between species (using a pooled regression line for all the Pinus pungens mother trees in the area) within their source areas showed no differences between species. Intraspecific differences did exist between the two sources of P. virginiana at both ages, and between young P. pungens within areas 4 and 27. When data for P. pungens were grouped for northern (areas 27, 26, 4) and southern (areas

1, 9, BB) sources, the regional differences were significant at the 5% level. Regressions of needle water potential (Ψ_n) on Ψ_s for P. pungens are shown in Fig. 22. The dashed straight line is the line of equal potential for needles and soil. It appears that there is no real difference between the northern and southern sources of "O" seedlings. The one aberrant observation (at Ψ_s = -50 bars) in the northern group probably led to the significant test of differences.

When Ψ_s is below -5 to -10 bars, Ψ_n is higher (less negative, meaning wetter) than Ψ_s. This gradient is the reverse of what is expected, as a plant potential lower than the soil potential is necessary for water uptake. As soil water content decreases, a greater potential difference is necessary to cause constant water uptake. The reverse gradient found could be caused by uptake of water from the saturated air at night. Such uptake, although slow, has been demonstrated for species of Pinus (Slatyer, 1967). A similar explanation involves possible condensation of water on needles in the moist chamber, which was lighted from outside by a desk lamp in the early part of the experiment. Heating of the chamber by the lamp resulted in condensation of water on the relatively cool pots, and probably on the needles. Use of the lamp was discontinued when this became evident, but some of the

Figure 22. Relationship between water potential of soil and of needles of *Pinus pungens* seedlings. Data points for Ψ_s above -10 bars are not plotted.


a. 3 to 5 Months
b. 15 to 17 Months
South
North
-30
-20
-10
-30
-20
-10
-10
-20
-30
-40
NEEDLE WATER POTENTIAL (bars)
SOIL WATER POTENTIAL (bars)

observations with relatively high Ψ_n may have resulted from it.

Probably the major cause of Ψ_n being less negative than Ψ_s is leaf resistance error in the psychrometer measurements (Boyer & Knipling, 1965). Diffusion resistance in needles of Pinus taeda, measured with a porometer, increased from 30 to 740 sec-cm^{-1} as needle water potential dropped from -5 to -20 bars. After plants were rewatered, this resistance increased from 70 to 510 sec-cm^{-1} over a similar drying cycle (Kaufmann, 1967). Presumably a similar relationship exists for the species used in this experiment. This increase in leaf resistance would slow vapor transfer in the psychrometer cup, causing the measured water potential to be above (wetter) than the actual one. This error would increase as Ψ_n decreased and leaf resistance increased. Resistance errors up to 12% were found for pines by Knipling (1966), working at potentials above -20 bars. To completely account for discrepancies found in this study, errors of at least twice this magnitude would be necessary. It seems likely that all three sources of error contributed to the relationship.

Inverted water potential gradients have been reported for pepper and sunflower, with plant potential up to 4 or 5 bars higher than that of the nutrient solution in which it was growing. This observation was explained as resulting from root pressure (Barrs, 1966). Since root

pressure occurs in plants rooted in wet soil (Kramer & Kozlowski, 1960) it is not a likely explanation in this case, since the reverse potential gradient increased as the soil became dryer.

Younger plants had potentials more above soil potentials than the older ones, possibly due to a higher potential threshold for stomatal closure. Also, since primary needles of pines are less cutinized, have thinner epidermal walls (Bormann, 1958), and have a higher surface to volume ratio, water could be absorbed more easily and a given amount of absorbed water would affect the overall potential of the needle more than for an older one.

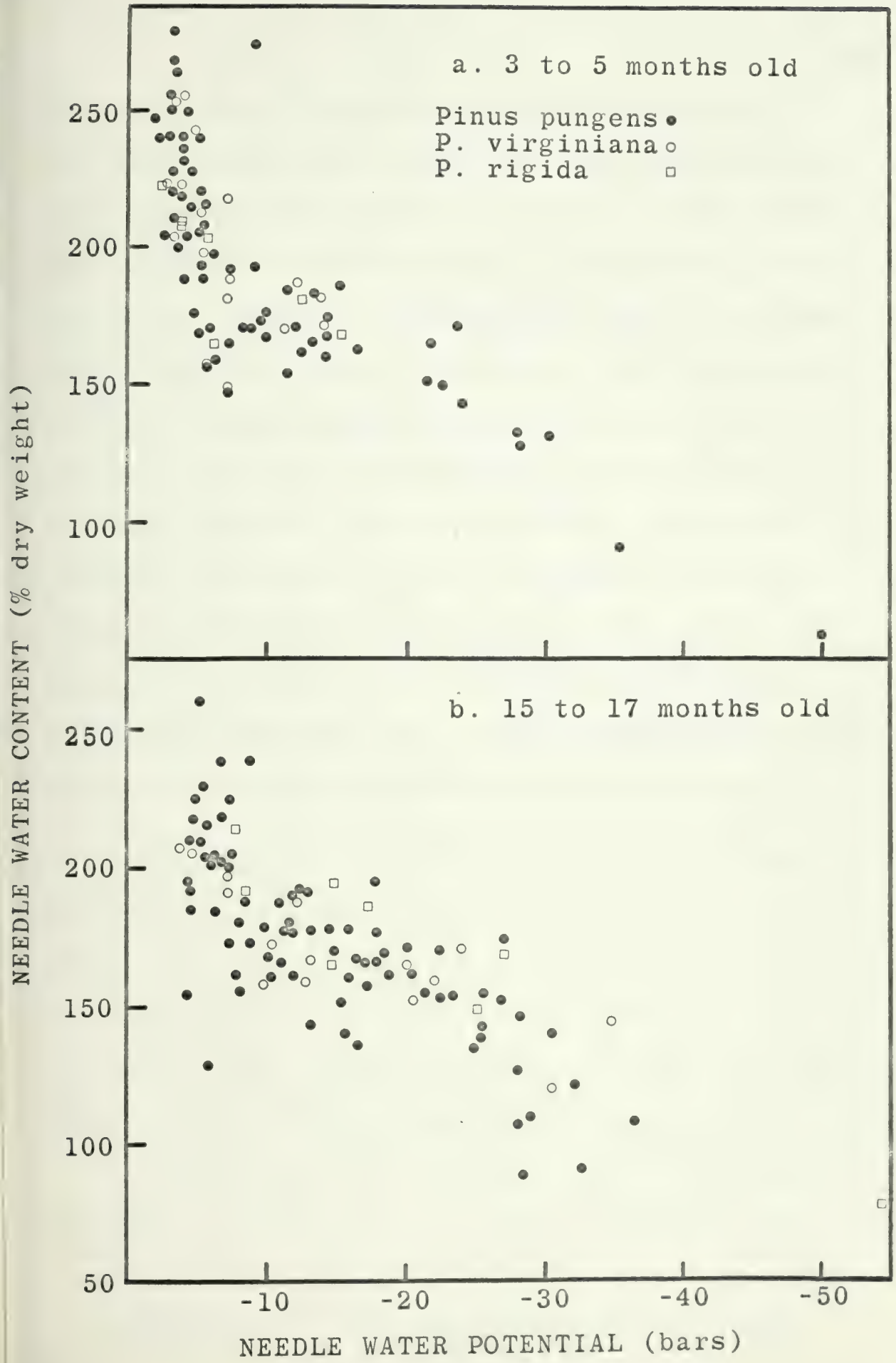
Psychrometer equilibration for drier needle tissue and soil was quite slow, usually taking 12 to 15 hours. Except in a few instances, especially with very dry soil, all determinations continued until the change in psychrometer read-out amounted to 0.1 bar per hour or less.

Respiration errors, corrected with the double thermocouples, were calculated, and varied widely at high needle potentials. For "Y" seedlings, errors up to 26 percent were found, although most were less than 10 percent. Maximum percent error decreased as potential decreased, but the average changed very little. Older seedlings showed no trend in size of error with potential, and almost all errors were below 10 percent.

Water content:water potential relationship of needles. The relationship between water content of the needle sample used for potential measurement, expressed as percent of dry weight, and needle water potential was determined for all sources of seedlings. A good relationship would be useful in future experiments, allowing estimates of Ψ_n from needle moisture content. Scatter in the data was too wide for this use, and no statistical comparisons between sources or species were made. However, the data plotted in Fig. 23 illustrate this relationship. It appears from Fig. 23 that older Pinus rigida needles have a higher water content than the average of the other two species throughout the potential range considered. Stated differently, it appears that they can lose less water before reaching a given level of water stress.

Transpiration:Soil Moisture relationships. The water lost by each seedling during each of the two days prior to sampling was determined and the results expressed as loss per gram dry weight of needles (or per gram dry weight of total top, for "Y" seedlings). From hygrothermograph charts, vapor pressure deficit (VPD) in inches of mercury was determined every 2 hours and plotted over time. The number of "inch-hours of VPD" between weighings, an estimate of the total evaporative potential of the air

Figure 23. Relationship between needle water content and needle water potential of 3 pine species.


a. 3 to 5 months old
Pinus pungens
P. virginiana
P. rigida
b. 15 to 17 months old
NEEDLE WATER CONTENT (% dry weight)
250
200
150
100
50
-10
-20
-30
-40
-50
NEEDLE WATER POTENTIAL (bars)

during the period, was determined by planimetering the area under the VPD curve. Water loss was finally expressed as grams water loss per gram dry weight per inch-hour of VPD. Correcting for the evaporative potential should allow more accurate comparison of measurements taken on different days. Regressions of water loss on soil water content were computed, and were compared as described for the plant potential:soil potential regressions. No differences were found when water loss of the day previous to sampling was used to estimate transpiration. The average of both days showed some differences. Older *Pinus pungens* and *P. rigida* differed at area 4, and the two sources of *P. virginiana* differed for older seedlings. A more intensive investigation of transpiration will be reported in the next section.

Experiment T. Because loss of water by individual plants was measured for only two days in Experiment D, variation between individuals is not separable from that caused by the drying of the soil or by different conditions on different days. Repeated measurements made on the same trees as they dried should give a better relationship.

One replication of both ages of the "D"-planting was used. It was broken into 4 groups of each age, each group with one plant from each of the 13 mother trees. The position of groups on the greenhouse bench and of pots

within groups was changed after every weighing.

Pots were saturated and covered as in experiment D. They were weighed every 2 days, between 8 and 11 p.m. VPD inch-hours for each period was calculated as before. When soil moisture decreased enough that water loss had become small (soil moisture of 3 to 5 percent), 20 ml. of water was added to the cup. At the next weighing, a new set of measurements was started.

At the end of the experiment, the weight and moisture content of the soil, the wet weight of the pot plus the seedling, and needle dry weight were determined. Assuming no significant change in plant weight over the 26-day measurement period, the percent soil moisture was calculated for all dates of weighing. From the soil moisture:soil water potential relationship determined in experiment D, the soil water potential was estimated.

Water loss in grams per gram dry weight per inch-hour was calculated as before. Regressions of water loss on soil moisture contents were determined, and differences analyzed as in experiment D. Plotting the data showed that periods with unusually low VPD inch-hour totals had much higher rates of evaporation than most. During these periods of low evaporative demand, absorption is better able to keep up with water loss, and much more of the potential for evaporation can be fulfilled by the plants,

giving higher rates per unit of evaporative demand. On days with high VPD, rate of water absorption limits transpiration and the extra inch-hours of VPD cause no increase in water loss. To remove much of the variation from this source, only periods with 13 or more inch-hours of VPD were used in calculations, eliminating 3 periods with 9.5, 7.1, and 8.4 inch-hours. To check for differences in dry soil, separate regressions were done for data with soil moisture below 7 percent (equivalent to about -8 bars in "Y" soil and -11 bars in "O" soil).

Water loss differences significant among "Y" plants included those between individuals of *Pinus pungens* at areas 4 and 27, and between northern and southern areas (South was areas BB, 1 and 9; North was areas 4, 27 and 26). The two sources of *P. virginiana* differed. Differences between species occurred in area 1, and in area 4 between *P. pungens* and *P. rigida*. Regression lines for southern and northern Table Mountain pine and for all species at areas 1 and 4 are plotted in Fig. 24. The southern trees apparently lost less water at high and very low soil moisture contents. At area 1, *P. virginiana* lost more water at higher moisture contents. However, between about 10 and 5 percent soil moisture (about -4 to -20 bars), it lost less. At area 4 there was no significant difference

between P. pungens and P. virginiana, or between the latter and P. rigida. P. rigida lost more water than Table Mountain pine at all soil moisture levels examined.

In older seedlings, similar differences appeared. P. virginiana at area 1 differed from one of two Table Mountain pines. At area 4 all three species differed from each other. Among Pinus pungens sources, individuals within areas 1 and 4 differed, as did north-south groups. Regression equations of groups showing significant differences are plotted in Fig. 25a-25c.

Data for soil moisture below 7 percent showed few differences, probably due to fewer data and the fact that large differences were at the higher soil moisture levels. Separate regressions fitted the various Pinus pungens sources better than a single pooled regression, as also appeared in the total data for both ages, but no smaller groups appeared to differ. P. virginiana at area 4 differed from the Table Mountain pine in the area, however. (See Fig. 25d).

Northern sources of "O" seedlings lost moisture somewhat faster at higher soil moisture levels. Water loss of P. virginiana at area 1 was more than one of the Table Mountain pines, and the same as the other. At area 4, P. virginiana had higher water loss at very high soil

Figure 24. Water loss of six to seven month old seedlings as affected by soil moisture. Soil water potentials at 16, 12, 8, and 4 percent, respectively, are -0.5, -1.5, -6, and -32 bars. a) *Pinus pungens*, north and south. b) *P. pungens* and *P. virginiana* from area 1. c) *P. pungens*, *P. virginiana* and *P. rigida* from area 4.

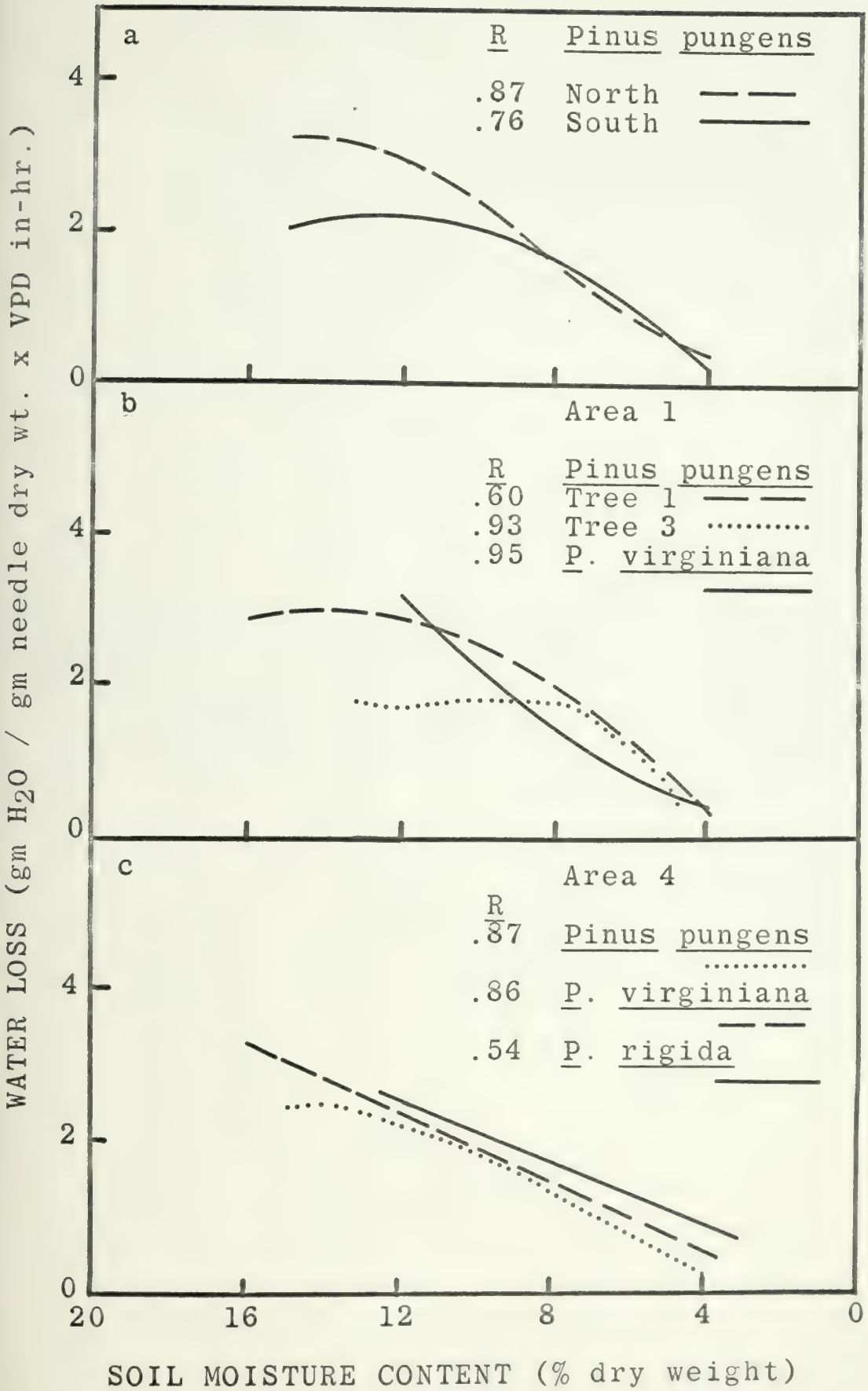
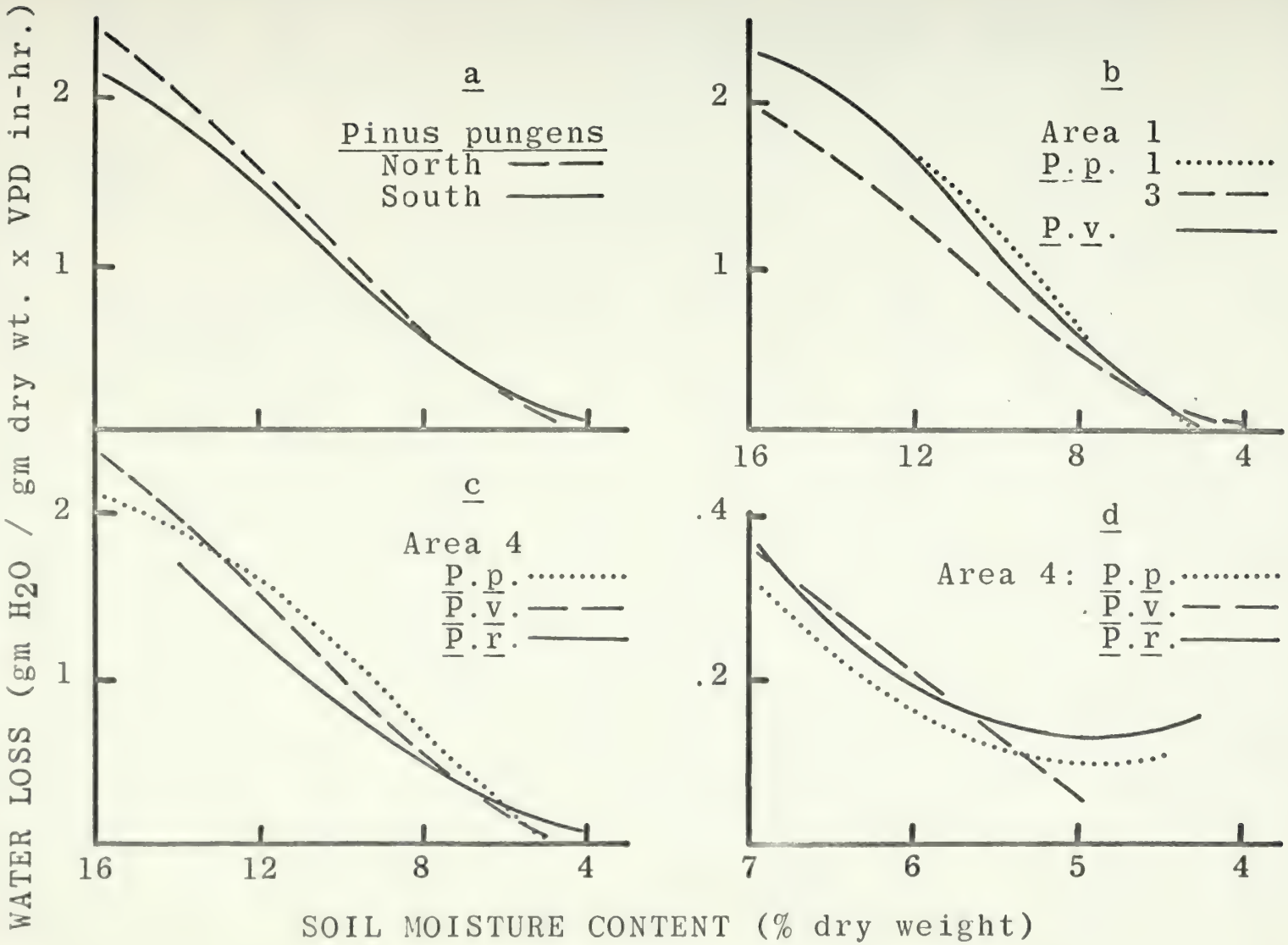

a
R
Pinus pungens
.87 North
.76 South
b
Area 1
R
Pinus pungens
.60 Tree 1
.93 Tree 3
.95 P. virginiana
c
Area 4
R
.87 Pinus pungens
.86 P. virginiana
.54 P. rigida
WATER LOSS (gm H2O / gm needle dry wt. x VPD in-hr.)
SOIL MOISTURE CONTENT (% dry weight)
0
2
4
20
16
12
8
4
0

Figure 25. Water loss of 18 to 20 month old seedlings as affected by soil moisture. Soil water potentials at 16, 12, 8, and 4 percent, respectively, are -0.5, -2, -8, and -40 bars. a) *Pinus pungens*, north and south. b) *P. pungens* and *P. virginiana* at area 1. c) *P. pungens*, *P. virginiana*, and *P. rigida* at area 4. d) Same as c, at low soil moisture only.


WATER LOSS (gm H2O / gm dry wt. x VPD in-hr.)
a
Pinus pungens
North
South
b
Area 1
P. p. 1
3
P. v.
c
Area 4
P. p.
P. v.
P. r.
d
Area 4: P. p.
P. v.
P. r.
2
1
.4
.2
16
12
8
4
7
6
5
SOIL MOISTURE CONTENT (% dry weight)

moisture levels, but lost somewhat less at lower levels. *P. rigida*, unlike the "Y" seedlings, lost less water except at low soil moisture.

Discussion. It appears that small differences in response to water stress may exist between sources of *Pinus pungens* and between species. No differences in reaction of needle water potential to soil water potential were found. However, water loss seemed higher for northern sources of *Pinus pungens* compared to southern sources, and for seedlings of *P. virginiana* of both ages at high soil moisture levels, compared to *P. pungens*. Young *P. rigida* lost more water than *P. pungens*, but older seedlings lost less except at low soil moisture levels. Although no extreme differences existed, or might really be expected to exist between such ecologically similar species, there is at least slight evidence that seedlings of Table Mountain pine, especially younger ones, are better adapted to dry sites than those of the other two species.

The rate of water loss from primary needles is considerably greater than from those seedlings with secondary needles. This could be expected, since primary leaves have relatively thin-walled epidermal cells and a thin cuticle (Bormann, 1958), and probably a higher surface to volume ratio than on mature needles. Their "provision for

controlling transpiration especially is much less developed" (Goebel, 1900: p. 153-154). These adaptations, which allow light saturation of photosynthesis at much lower intensities (Bormann, 1958) and higher actual photosynthetic rates (Wright, 1967), aid initial survival under low vegetation but would seem to be of least advantage on hot, dry, sparsely vegetated areas.

Many sources of Pinus pungens, especially "Y" seedlings, had a regression line of water loss on soil moisture which leveled off or even decreased at high soil moisture contents. Pinus pungens might be more susceptible to adverse effects of poor soil aeration at higher moisture contents.

Seedling Response to Increased Calcium and Magnesium

Pine species differ in calcium tolerance. Some may be excluded from calcareous soils (Mirov, 1967). Some species show deficiency symptoms at low calcium and magnesium concentrations, while others do not. Some species become chlorotic on calcareous soils, and Woodwell (1958) showed that seedling growth of one source of Pinus serotina was inhibited by 400 ppm calcium, below the maximum

concentrations which occur within its range. High calcium concentrations or pH above 6.5 directly reduce germination and seedling survival of Pinus echinata in culture and in nursery beds (Chapman, 1941). So, although pines tolerate a wide range of calcium concentrations in the soil, species do vary in their tolerance, and both excesses and deficiencies may affect the growth and distribution of species (Kramer & Kozlowski, 1960; Mirov, 1967).

The well-known example of edaphic limitation of plant distribution by serpentinite soils involves low calcium level as a principal limiting factor. Tolerance to this and other minerals which are deficient or are present in excessive quantities is necessary for survival. Some species and ecotypes are endemic to this soil type, but restricted to it, perhaps, by the more intensive competition on "normal" soils (Billings, 1957). Development of serpentinite races as in many herbaceous species was not found in 6-month old Pinus sabiniana seedlings (Griffin, 1965). However, Kruckeberg (1967) suggests that any differences in woody plants may appear well after seedling establishment, and found 26 months necessary for differences between response of serpentinite and non-serpentinite sources of P. contorta to develop.

Since Pinus pungens usually occurs on soils rather low in calcium, and was never seen on limestone areas, its response to increased levels of calcium and magnesium in the soil was examined. The other two pine species with which it usually occurs were also used for comparison, since the species might respond differently to high or low concentrations of these elements. To test the effect of higher levels, calcium and magnesium were added to area I soil. The amounts added were calculated to give a calcium concentration similar to a soil found on limestone within the range of P. pungens. Enough magnesium was added to keep the calculated Ca:Mg ratio the same as in the original soil.

Because high soil pH can cause poor mycorrhizal development through its effect on host nutrition (B. N. Richards, 1965), the effect of and on mycorrhizae was also examined. If Tamm's (1964) suggestion that nutrient tolerances of soil organisms may differ from those of trees is true for mycorrhiza-formers, information about relative response of mycorrhizae to increased lime could be of interest.

Area I soil collected March 28, 1966, was divided into two lots, one of which was sterilized by methyl bromide fumigation for 44 hours. To half of each of the

sterilized and unsterilized lots, a mixture of agricultural lime and $CaCO_3$ was added and very thoroughly mixed, to give calculated Ca and Mg concentrations of 5 and 2 millequivalents/100 grams (or about 2000 and 480 lb/acre, or 1000 and 240 ppm). Sterilized soil was designated as treatment "M", and natural soil as "N." Soil with lime added was called "L", and that without was called "O." A 2 x 2 factorial experiment, with treatments ML, MO, NL, and NO, was set up, with 10 pots per seed source in each of 4 replications. Plants were grown in 16-ounce foam plastic cups, randomly arranged within replications. Seed from *Pinus pungens*, *P. virginiana*, and *P. rigida* from sample area 4 were used. Soaked seeds were planted on April 13, 1966, in the greenhouse and pots moved outside five weeks later. On June 23, 1966, all pots were thinned to one seedling.

Characteristics of the experimental soils at the time the experiment began and when half the seedlings were harvested in October, 1966, are listed in Table 27. Chemical analysis was done by the North Carolina Department of Agriculture, using the same methods as for field soil samples.

To determine whether the response changed with time, half of each replication was harvested in October, 1966, about 6 months after planting, and the remaining plants in August, 1967, at 16 months.

Table 27

Soil characteristics of liming experiment soil treatments. (Means of 2 determinations except 0-month chemical characteristics, which are for 3 determinations.) "M"-treatments are on fumigated soil; "N" is unfumigated. "L"-treatments had calcium and magnesium added; "O" did not.

CHARACTERISTIC	TREATMENT AND AGE OF PLANTS (MONTHS)							
	NO		NL		MO		ML	
	0	6	0	6	0	6	0	6
Physical								
>2 mm (% of total sample)	57	--	54	--	60	--	59	--
Sand (% of < 2 mm fraction)	65	--	65	--	67	--	64	--
Silt (%)	17	--	18	--	16	--	18	--
Clay (%)	18	--	17	--	17	--	18	--
Chemical (of < 2 mm fraction)								
pH	4.5	4.1	6.0	5.5	4.3	4.0	5.8	5.5
Organic Matter (%)	1.8	2.3	1.9	2.8	1.8	2.3	1.8	2.5
Ca (lb/acre)	150	96	1553	1230	117	64	1218	1057
Mg (lb/acre)	20	28	196	228	23	19	172	240
P (lb/acre)	2.6	4.0	0.6	4.0	5.3	5.0	0.6	4.0
K (lb/acre)	114	66	104	55	122	66	122	55
Mn (lb/acre)	7.3	8.0	6.0	10.0	6.0	7.0	6.0	8.0
Nitrate (ppm)	--	0.5	--	0.5	--	0.0	--	0.0
Ammonium (ppm)	--	19	--	16	--	22	--	12

Speed of germination was about the same in all treatments, varying more with species than with treatment. Percent germination was about 10% higher in fumigated soils, but equal in limed and unlimed soils for Pinus pungens and P. virginiana. P. rigida showed no variation with treatment.

In June, 1966, the first differences between treatments appeared. Seedlings in the MO treatment were uniformly a much brighter green than other treatments. Unfortunately, nitrogen determinations at 0 months were not made. The MO treatment had a much higher phosphorus concentration than the others, however, possibly due to decomposition of the soil microorganisms killed by fumigation. This phenomenon lasted only a short time.

6-month old seedlings. In the early October, 1966, harvest, length of stem and of the largest root were measured, the number of branches and of secondary roots longer than 1 cm., and presence of mature needle fascicles was recorded. After washing, and drying at 67 C for 24 hours, shoots and roots were weighed.

Fresh roots were examined for mycorrhizae, which were grouped and counted. Rough morphological groupings used were type 1) black mycorrhizae; type 2) white, of small diameter, usually present in groups with large numbers of

highly ramified mycorrhizal tips radiating from a central point on the root; type 3) white, of larger diameter, usually single or bifurcate; type 4) white, similar to 3 but of smaller diameter; and type 5) dark, otherwise similar to type 2. Type 4 may be an immature stage of types 2 or 3, as morphological form and color of mycorrhizae may change with age. Type 1 is probably formed by Cenococcum graniformae, which has black hyphae from the onset of mycorrhizal formation (Trappe, 1967). This grouping is admittedly very rough, but precise enough to allow classification of the types found, and comparison of treatments and tree species.

Fumigation prevented mycorrhizal formation in about half the fumigated pots, with many more limed seedlings developing mycorrhizae than unlimed ones, in the fumigated soil. These mycorrhizae were mostly types 3 and 4, with an occasional type 5. Types 1 and 2, usually both, were present in all non-fumigated pots, along with an occasional type 5 or 3. Types 1 and 2 were in only one fumigated pot each. It appears that types 1 and 2 are formed by fungi present in the natural soil, whereas types 3, 4, and 5 are either absent or infrequent, and were introduced as contaminants.

Since the growth of seedlings in fumigated pots was obviously correlated with presence of mycorrhizae,

data were analyzed separately for treatments N and M. M treatments were further designated as inoculated (with mycorrhizae) or uninoculated ("I" or "U").

Nonfumigated treatments. Results were analyzed using multiple regression analysis with single degree of freedom contrasts assigned for replications, species, and liming, and for all possible interactions. Treatment means are shown in Table 28.

Height, total weight, and root weight were significantly different between limed and unlimed plants and between *Pinus pungens* and the other species. No interactions were significant. Numbers of lateral roots and weight of the top showed the same pattern, but *P. rigida* had values significantly greater than *P. virginiana*, besides the other differences. Root:shoot ratio (RSR) showed no differences between species or liming treatments, but one interaction was significant. RSR of *P. rigida* and *P. pungens* decreased slightly with liming, while *P. virginiana* increased. Length of the largest root increased with liming and *P. pungens*' was longer than the other species. Root length of *P. rigida* showed much less response to liming than *P. virginiana*.

The number of mycorrhizae on the root system increased with liming. *P. virginiana* had fewer than the other species. The number of types of mycorrhizae was higher

Table 28

Selected treatment-by-species means for liming experiment, 6-month old seedlings. (Under fumigated treatments, the upper value is for mycorrhizal plants, the lower for non-mycorrhizal plants.) "L"-soils had calcium and magnesium added; "O"-soils did not. RSR = Root:shoot ratio. ODW = Oven-dry weight.

Characteristic	*P. pungens*		*P. virginiana*		*P. rigida*	
	L	O	L	O	L	O
Non-fumigated soil						
Total ODW (gm)	.51	.42	.38	.26	.48	.31
Top ODW (gm)	.25	.20	.18	.13	.25	.15
Root ODW (gm)	.26	.22	.20	.13	.23	.16
RSR	1.05	1.12	1.16	1.06	.95	1.16
# Lateral Roots	19	15	14	13	17	14
Length longest root (mm)	575	500	450	292	377	335
Height (mm)	85	80	74	68	76	66
# Mycorrhizae	110	97	97	73	116	103
# Mycorrhizal Types	2.7	2.2	2.8	2.3	2.5	2.1
# Branches	1.6	1.3	1.0	.4	.8	.2
Fumigated soil (Top value is for mycorrhizal plants, lower is for non-mycorrhizal plants)						
Total ODW (gm)	.70	.54	.39	.27	.57	.42
	.32	.26	.24	.18	.24	.18
Top ODW (gm)	.40	.30	.21	.15	.32	.24
	.16	.14	.10	.08	.12	.10
Root ODW (gm)	.30	.24	.18	.12	.25	.18
	.16	.12	.13	.09	.12	.08
RSR	.82	.82	.88	.79	.87	.75
	1.02	.89	1.23	1.09	1.03	.84
# Lateral Roots	24	18	22	17	22	18
	21	16	21	17	22	14
Height (mm)	100	91	85	71	93	97
	63	58	60	51	53	53

in limed soil than unlimed, and P. virginiana had more types than P. rigida. Numbers of various types of mycorrhizae were compared also (Table 29). Percent of mycorrhizae per plant which were of types 1 and 2, types apparently present in natural soil before fumigation, was determined. In unlimed soil, an average of 98, 96, and 96 percent of mycorrhizae per plant were of these types, on P. pungens, P. virginiana, and P. rigida, respectively. In limed soil, 86, 90, and 68 percent were of types 1 and 2, in the three species. Species differed in percent of these types at the 5% level, and soils at the 1% probability level. To determine any species differences in abundance of natural mycorrhizal types, the ratio of numbers of type 1 to type 2 was computed for all plants. Although this varied widely from plant to plant, species differences in the average ratio were similar on limed and unlimed soil. Six plants (all P. rigida) lacking type 2, and therefore with infinite ratios, were omitted from the averages. P. pungens, P. virginiana, and P. rigida, respectively, had the following average ratios: 4.61, 3.58, and 8.44 for unlimed soil, and 4.49, 3.23, and 8.60 for limed soil. Species differences are highly significant. However, the absolute number of various types of mycorrhizae does change, differently with species. Liming caused no change in numbers of types 1 and

2 in *P. pungens*, but caused an increase in Virginia pine and a large decrease in pitch pine (Table 29). Although the interaction of species and soil is not significant for type 1 or type 2, it is significant for their sum, the total number of "natural" mycorrhizae.

Table 29

Average numbers of mycorrhizae per seedling by types, in the liming experiment, unfumigated soil. "L"-soils have added calcium and magnesium; "O"-soils do not.

Species	*P. pungens*			*P. virginiana*			*P. rigida*		
Type	1	2	other	1	2	other	1	2	other
O soil	73	22	2	51	19	3	84	15	4
L soil	70	25	16	61	25	11	61	10	46

Under the growth conditions of these plants, the mycorrhizal condition, as well as other plant characteristics, was species specific, and varied with liming. Liming increased the total number of mycorrhizae and number of mycorrhizal types present, and allowed formation of a higher proportion of them by apparent "invaders." It did not change the ratio of the two most common and presumably natural types, but changed their absolute frequency.

It appears that adding calcium and magnesium to the soil increased most measures of growth recorded for all

species and, at the levels used, enhanced mycorrhizal formation. The conditions used, a very limited soil mass and plentiful water, might have affected the response to lime, and this experiment showed only that liming itself increased plant growth. Its effects under limited moisture, or on drought resistance, would be interesting to know.

Fumigated treatments. The analysis of these data was complex, involving different numbers of inoculated and uninoculated seedlings. Data were treated by using a series of multiple regressions run with factors in different order. Sums of squares for different factors and interactions corrected for the appropriate other factors, were extracted from the regressions and used in an analysis of variance table. Treatment means are shown in Table 27.

Lime, and especially presence of mycorrhizae, significantly increased total weight and root weight. *Pinus pungens* was heavier than the other species. Shoot weight showed the same pattern, with *P. rigida* significantly heavier than *P. virginiana* also. *P. virginiana* had a much higher RSR than the other species. RSR was increased by lime and decreased by presence of mycorrhizae. One significant interaction indicated that absence of mycorrhize increased RSR of *P. virginiana* more than that of the other species.

Mycorrhizae increased height, with lime showing no

effect. P. pungens was taller than the other species. Absence of mycorrhizae reduced height of P. rigida more than that of P. virginiana. Lime, but not presence of mycorrhizae, significantly affected the number of lateral roots. The number and types of mycorrhizae were not analyzed. However, liming fumigated soil increased the number present and the percentage of plants with mycorrhizae.

All treatments. Analyses run on all data indicated that P. pungens and P. rigida had larger percentages of plants with needle fascicles present (53 and 45 percent) than P. virginiana (11 percent). Liming had no effect. P. pungens develops almost 1.5 branches per plant, compared with 0.9 for P. virginiana and 0.5 for P. rigida. Plants in limed soils have almost twice as many as those in unlimed soils.

Survival at 13 months: On May 18, 1967, remaining plants were scored for survival. Analysis of number of seedlings surviving indicated seedlings in limed and non-fumigated soil survived better. There was no significant interaction or difference between species. Means are shown in Table 30. The survival in fumigated soil is probably highly correlated with the establishment of mycorrhizae. Those seedlings without mycorrhizae seldom grew beyond the "rosette" stage, with a tuft of primary needles just above

the cotyledons.

Table 30

Percent survival for liming experiment, after 13 months. "L"-soils have added calcium and magnesium; "O"-soils do not.

Species	Treatment			
	Fumigated		Unfumigated	
	O	L	O	L
P. pungens	21	89	100	100
P. virginiana	40	95	100	95
P. rigida	32	74	77	92

Shoot growth at 16 months. In August, 1967, the surviving plants were harvested and height and oven-dry-weight of the top determined. Results were similar to those found at 6 months. Height and top weight differences were larger, but in about the same proportion, in most cases, as at six months. The only major difference was that *Pinus rigida* showed a definite height increase due to liming in the fumigated treatments, which was not present at six months.

Discussion. Some soil chemical properties changed in the first six months, with pH and calcium content, and especially potassium, decreasing. Organic matter, magnesium, manganese, and phosphorus all increased. Uptake by the

plants, loss by leaching, and changes in availability (absorption on or incorporation into soil particles, changes in chemical form with pH change, or further breakdown of agricultural lime) may account for this.

Addition of lime to unfumigated soil caused somewhat smaller increases in weight, height and root length of *Pinus pungens* than of the other species, although this difference was not statistically significant. Lime caused largest changes in root systems of *P. virginiana* and shoots of *P. rigida*. Types of mycorrhizae and changes caused by liming appear to be species characteristics. The situation in fumigated soil was similar in some ways. Although liming caused more robust and apparently healthier plants of all species, Table Mountain pine may have derived less benefit from it than the other species.

Differences between "I" and "U" plants in fumigated soil illustrated the common observation that pines need mycorrhizae to grow in poor soils. Trees with mycorrhizae were taller, heavier, and have more shoot weight per unit root weight. *P. virginiana* did, relatively, the best without mycorrhizae. The weight of other species more than doubled with mycorrhizae, while *P. virginiana* increased by 50-60 percent. Similar height differences occurred. The number of lateral roots, which increased markedly in fumigated soil

and increased with liming, was unchanged by the presence of mycorrhizae.

This experiment illustrated species differences besides reaction to liming. Table Mountain pine, as expected from its larger seed, had the tallest, heaviest seedlings, with the longest root and the most lateral roots and branches. It seemed to develop needle fascicles earlier than *P. virginiana*.

The response of root-shoot ratios (RSR) varied in this experiment. *P. virginiana* RSR varied directly with seedling weight in all cases, similar to the reaction found by Ledig & Perry (1965) for 60-day old *P. taeda*. *P. rigida* followed this pattern in fumigated soils only. *P. pungens* followed it only in the absence of mycorrhizae. The sign of the correlation between RSR and weight was also not directly related to the plant size. There seems to be some confusion about the relationship of RSR and plant weight of pines. Ledig & Perry (1965) state unequivocally that "shoot-root ratio decreases with total plant weight for woody plants", (*i.e.* *root-shoot* ratio *increases* with weight), but consider mostly experimental data from even-aged seedlings. They conclude that the departures from this allometric growth relationship are caused only by "drastic treatment" and emphasize that care must be used in

interpretation of root-shoot changes from experimental treatments. Monk (1966) found the opposite relationship with larger trees (of different ages?) from natural stands. It appears that attempts at interpretation in the present case may be futile, with the complicating factors of limited space for root growth and the complex relationships discussed above. It may be possible to say, however, that mycorrhizae increase the efficiency of water or mineral absorption, as has often been found, since the interdependence of root and shoot tends to maintain a relatively efficient balance between the two plant parts (Kramer & Kozlowski, 1960). Also, it can be at least suggested that Pinus pungens seemed to maintain a somewhat more stable (or less adaptable?) root-shoot ratio than the other species.

Effects of Temperature

The distribution of Pinus pungens, which is limited mainly to the warmer slopes where it occurs, suggests that the species is limited by temperature. On a larger scale, it is relatively abundant in the Valley-and-Ridge province, but has been found in only a few locations west of the Allegheny Front in West Virginia, where temperatures average

6 to 7 F lower and growing seasons are shorter (Clarkson, 1966). It is also quite rare on the Piedmont surrounding the monadnocks where it occurs. Probably, effects on different phases of the life cycle, some at high and others at low temperatures, help limit its distribution. The effect of temperature on reproduction and seed germination has already been discussed. Its effect on early seedling development and later seedling growth and characteristics were investigated also.

Early seedling development. Seedlings were grown in the soil troughs of the temperature gradient bar and chamber used for germination experiments. Coarse white sand in plastic sandwich bags was placed in the trough. The 11 bags used in the gradient were separated by plywood dividers. Temperature measured 1 inch deep in the center of each bag with a thermistor probe was used as the station temperature for that bag. Water was added as necessary to keep the sand wet to the top. Germinating seed was placed just below the surface of the sand. Equal numbers of seeds of each seed source or of each species were placed in each bag, in 3 rows parallel to the direction of the temperature gradient. Position of row for each seed source was randomized in each bag.

In the first two experiments, seedlings were allowed to develop for a given time. Length of hypocotyl and root were measured, average dry weight per plant was determined and the species scored for stage of development. Seeds of three species were used, from area 4 and from Smith Mountain, Virginia. Dry weight, root length, stage of development reached, and, from Smith Mountain, hypocotyl length, varied with temperature. Species differences existed only in hypocotyl length. Patterns of dry weight suggested that the light gradient, from high at both ends to low in the middle, affected seedling growth, as average light intensity was only about 500 ft.-candles (Barbour & Racine, 1967). Similar results were found with Larrea (M. G. Barbour, personal communication, 1967). Therefore, only very early development was used in later experiments, so that photosynthetic differences would have minimal effect.

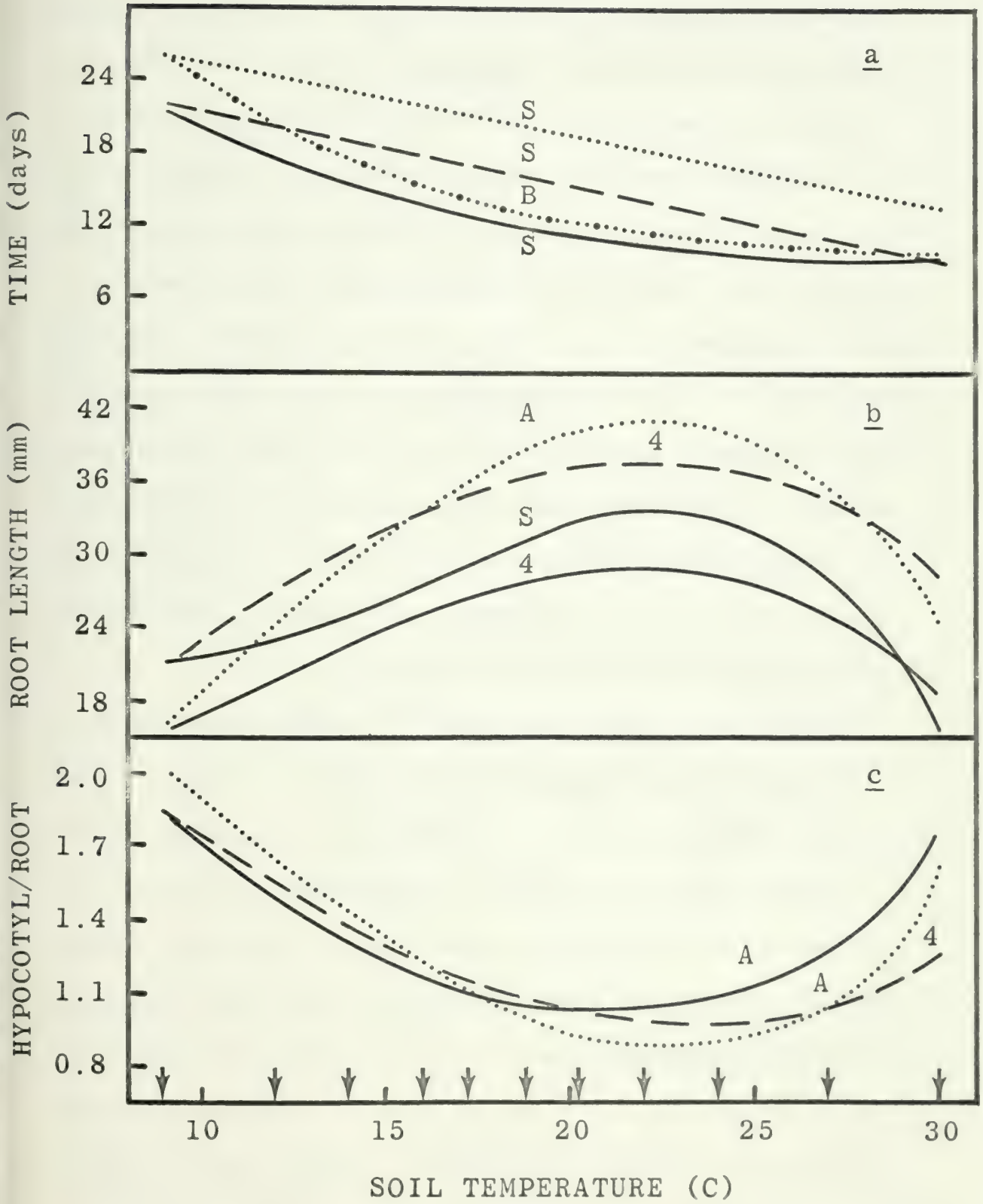
In experiment H4, seedlings were allowed to develop until their seed coat was pushed off the cotyledons, a period during which most dry weight accumulated was presumed to be from reserves stored in the seed. Age, length of root, and length of hypocotyl were recorded. Seeds from three species were used, from Area 4 and Smith Mountain. Six seeds of each species from one source were planted in each bag. Which trough a certain source at a given

temperature occupied was randomized. Seeds, before transfer to the troughs, had been on sand at a common temperature until a majority started to germinate. Seedlings were removed at least daily as they developed. Data from the first five seedlings in each species-source-temperature group were used, where all six did develop. In other groups all were used.

Multiple regression techniques were used to determine the effects of source, species, and temperature on length of root, of hypocotyl, and total length, the ratio of hypocotyl to root length, and age when the seed coat separated. When data from sources were analyzed separately, significant differences between *Pinus pungens* and the other species, and between *P. virginiana* and *P. rigida*, were found for all length measurements at area 4. At Smith Mountain, *P. pungens* differed from other species in age and in the length measurements. *P. virginiana* was different from *P. rigida* only in root length.

When species were analyzed separately, *P. pungens* varied with source for age only. *P. virginiana* sources varied in all factors, and *P. rigida* in hypocotyl and root length, and in age. Regression lines of time-to-develop (age), root length, and ratio of hypocotyl to root length on soil temperature are plotted in Fig. 26.

Figure 26. Response of early seedling growth to soil temperature. Temperature at centers of experimental stations shown by arrows on the temperature axis. A = area 4 and Smith Mountain data pooled, 4 = area 4, S = Smith Mountain, B = all species at area 4 pooled. Solid line = *Pinus rigida*, dashed line = *P. virginiana*, dotted line = *P. pungens*. a) Time for seedlings to develop enough to shed seed coat. b) Root length at time of seed coat shed. c) Ratio of hypocotyl:root length at time of seed coat shed.


a
TIME (days)
24
18
12
6
S
S
B
S
b
ROOT LENGTH (mm)
42
36
30
24
18
A
4
S
4
c
HYPOCOTYL/ROOT
2.0
1.7
1.4
1.1
0.8
A
A
4
10
15
20
25
30
SOIL TEMPERATURE (C)

Groups of data with no significant change with temperature are not plotted. Lack of significant variation with temperature by P. virginiana from Smith Mountain might have been due to poor germination, causing small sample size. Roots of P. rigida were shorter than those of other species at almost all temperatures, but it appeared to be less affected by temperatures than the other species. P. pungens seemed to be most affected by temperature, having a shorter root than P. virginiana at high and low temperatures, and a longer one from 16 to 28 C. Minimum hypocotyl to root length ratio occurred about the same temperature as maximal root length (since hypocotyl length varied little with temperature), except for P. rigida.

Length of root would seem to be important in early seedling establishment on dry, warm slopes. This would make P. rigida appear to be at a disadvantage on these areas. A minimum ratio of top size to root length, especially during seedling establishment, would also seem to be the optimal condition for surviving on drier areas. If the hypocotyl to root ratio estimated this, it appears that the other species would be favored over P. rigida at higher temperatures.

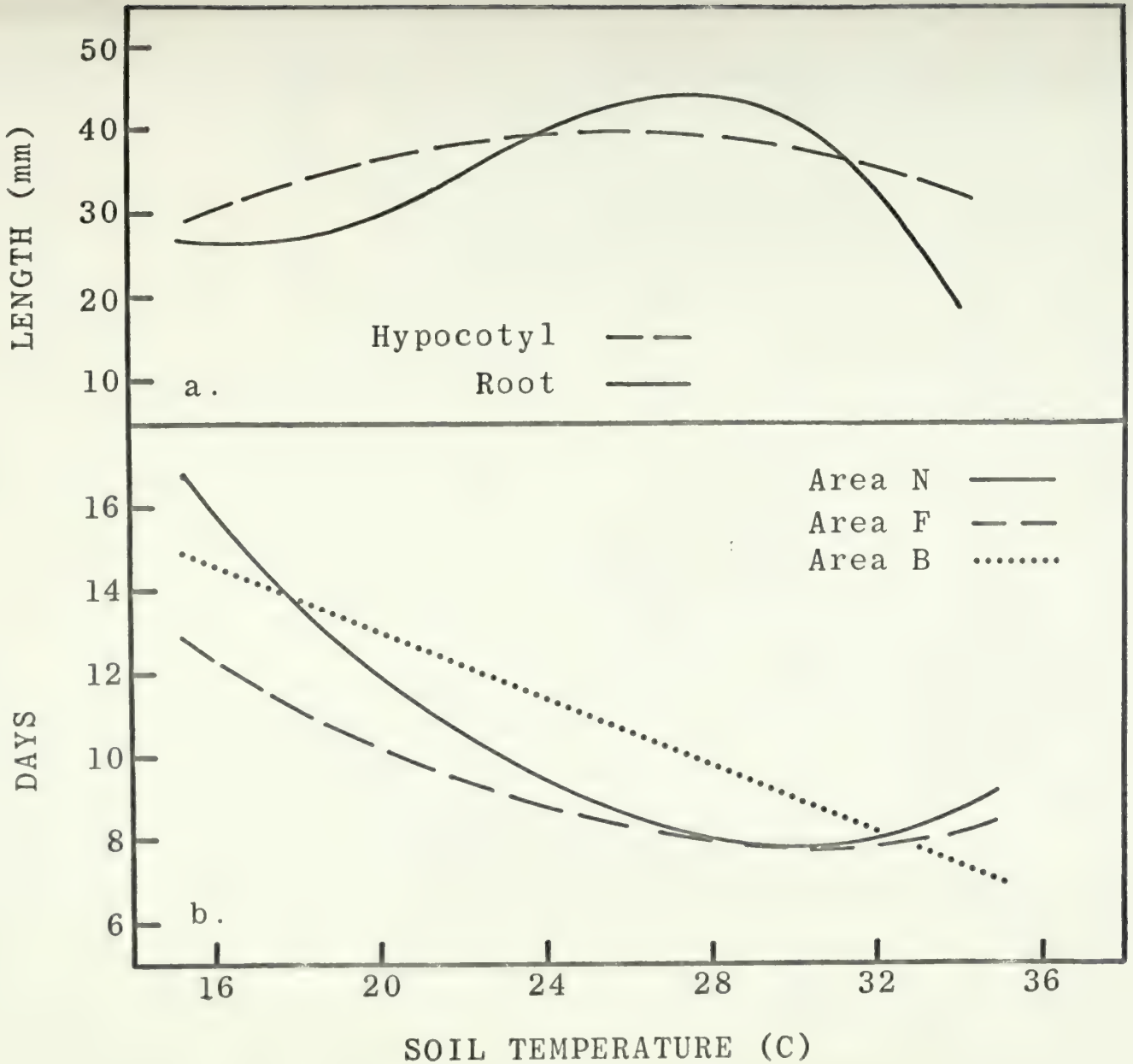
The experimental conditions of adequate (possibly excessive) water, relatively nutrient poor substrate without

natural microorganisms, constant temperature, dim light, and an air temperature gradient less well-developed than that of the soil could radically alter responses from those found in the field. However, knowing the species characteristics and presumed temperature responses shown here should give at least some clues to the natural reactions.

Experiment H3 compared three sources of Table Mountain pine used in germination experiment G8, areas N, F, and B. It was carried out similarly to H4, except that a different temperature range was used and oven dry weights were determined. Five seeds of sources F and B were used. Seed from N was limited and only three seeds per station were available. Data from all seedlings reaching the stage of losing the seed coat were used.

No statistical differences between sources were found. Regression equations with temperature were computed for all characteristics and all sources. Regressions of characteristics changing significantly with temperature are shown in Fig. 27. Age changed significantly with temperature at all sources. Root, hypocotyl, and total length varied significantly only for source F. Hypocotyl:root length ratio and seedling weight showed no significant change with temperature.

Figure 27. Response of some seedling characteristics of *P. pungens* to soil temperature. a) Hypocotyl and root length, area F. b) Time for seedlings to develop enough to shed seed coat, areas N, F, and B.


LENGTH (mm)
50
40
30
20
10
a.
Hypocotyl
Root
DAYS
16
14
12
10
8
6
b.
Area N
Area F
Area B
16
20
24
28
32
36
SOIL TEMPERATURE (C)

Experiment W: Interaction of liming and temperature. Methods. Distribution depends not only on seedling establishment but also on later growth and survival. To investigate reactions to cold by older plants, seedlings were exposed to low temperatures after initial establishment and growth in the greenhouse. Soil from the six-month harvest of the liming experiment was used. Keeping limed and unlimed soil separate, all large aggregates were broken and the fumigated and unfumigated soil thoroughly mixed and placed in 16-ounce foam plastic cups wrapped with aluminum foil. Soils were designated "L" and "O" for limed and unlimed. Chemical characteristics of soils are shown in Table 31. Half of each soil group was designated "N", and the rest "S", for the lower and higher temperature treatments. Twelve seed sources were used, two trees each of *P. pungens*, *P. virginiana*, and *P. rigida*, from area 4 and Smith Mountain, Virginia. Four cups of each tree-source-species-temperature-soil treatment were used. Three seeds, soaked for 24 hours, were planted in each cup on February 3, 1967. Data from all seedlings were used. On April 21, all plants were moved into a controlled temperature chamber constructed from an island-type food freezer, described in detail by Billings *et. al.* (1968). A fourteen-hour light, warm period

Table 31

Chemical characteristics of limed (L) and unlimed (O) soils from temperature and liming experiment (Expt. W). Means of 4 determinations ± 1 standard deviation.

Characteristic	Soil	
	L	O
pH	5.6±.3	4.5±.1
Organic matter (%)	2.75±.31	2.90±.13
Calcium (lb/acre)	1568±244	328±40
Magnesium (lb/acre)	339±34	61±11
Potassium (lb/acre)	101±0	101±0
Phosphorus (lb/acre)	0.0±0.0	0.5±1.0
Manganese (lb/acre)	7.0±1.1	4.0±0
Nitrate (ppm)	4.25±2.41	1.00±0.00
Ammonium (ppm)	7.50±.58	7.25±.58

was used, with maximum temperature during the light at 77 F (25 C) and minimum during dark period of 60 F (15.6 C). After May 12, photoperiod was reduced to 12 hours and temperature gradually lowered. On May 23, height of all plants was measured, and the low-temperature group placed in a similar chamber. Plants were watered every two days. Air and soil temperatures were measured with Moeller thermographs. Due to mechanical problems, "day" temperatures in the warmer chamber varied more than expected, reaching 82 F one day. Mean maximum light period temperatures for the warmer chamber were ($\pm$ 1 standard deviation) 64.6 $\pm$ 7.0 F (18.1 C) in the air and 65.8 $\pm$ 6.1 F (18.7 C) in the soil. Mean minimum temperatures for the dark period were 42.5 $\pm$ 1.7 F (5.8 C) and 44.5 $\pm$ 1.7 F (6.9 C). In the colder chamber, maximum temperatures were 56.0 $\pm$ 1.8 F (13.3 C) and 54.2 $\pm$ 1.5 F (12.3 C) for air and soil, and minimums were 34.2 $\pm$ 1.2 F (1.2 C) and 33.2 $\pm$ 1.5 F (0.7 C). Light intensity at plant level varied between about 1700 and 2000 foot-candles. Plants were harvested from August 15-18, at 6-1/2 months old, after almost 3 months at different temperature regimes. Height and length of longest root were measured, and oven-dry weight of top and root determined. Since the most noticeable difference in plants was color, the percent of green needle surface was estimated. The

number of spirals (approximately whorls) of dead, dry needles at the base of the crown was counted. Results were analyzed by analysis of variance technique. Multiple regression analysis was also used to break significant factors and interactions into individual degrees of freedom for more detailed analysis. In regression analysis, number of plants per pot and original height were used as covariates.

Results. Means are in Table 32 and F-values for analysis of variance are shown in Table 33. "Environment" is a temperature by soil treatment. "Trees" represents the difference between the two mother trees of a species from a source, and is a measure of intrapopulation variation. In all cases, values analyzed are the means of all seedlings in an individual pot. The analysis of variance represents the results of the total growth conditions on the plants. The regression, in which height before temperature treatment is used as a covariate, comes closer to representing the change during temperature treatment. Results of the regression are discussed below.

Height: The covariate, height-before-treatment, removed most of the differences between species and sources shown as significant in Table 33. Little change in height occurred during treatment. Liming alone was significant (5% level) after effect of initial height was removed. It

Table 32

Treatment means for temperature and liming experiment (Expt. W). Each figure is the mean of eight pot means, four each from two mother trees. "L"-soil had calcium and magnesium added; "O"-soil did not.

				AREA 4			SMITH MOUNTAIN		
Characteristic	Units	Temperature	Soil	*P. rigida*	*P. pungens*	*P. virgin.*	*P. rigida*	*P. pungens*	*P. virgin.*
Height	mm	Low	O	46.1	52.1	55.2	42.9	53.4	51.5
			L	50.5	59.6	57.7	45.9	58.4	53.4
		High	O	49.2	47.2	52.5	47.4	53.1	48.4
			L	54.9	56.1	54.6	43.8	60.2	52.7
Root length	mm	Low	O	219	261	218	234	267	191
			L	200	227	200	190	197	199
		High	O	253	294	218	268	304	197
			L	189	290	219	264	248	202
Shoot weight	gm	Low	O	.064	.075	.059	.058	.087	.056
			L	.077	.097	.080	.074	.106	.070
		High	O	.078	.079	.068	.075	.109	.055
			L	.107	.110	.086	.081	.128	.077
Root weight	gm	Low	O	.077	.081	.070	.075	.091	.061
			L	.062	.080	.068	.057	.072	.055
		High	O	.126	.117	.096	.122	.144	.078
			L	.110	.118	.084	.087	.111	.071

Table 32 (continued)

Characteristic	Units	Temperature	Soil	AREA 4 *P. rigida*	AREA 4 *P. pungens*	AREA 4 *P. virgin.*	SMITH MOUNTAIN *P. rigida*	SMITH MOUNTAIN *P. pungens*	SMITH MOUNTAIN *P. virgin.*
Root:shoot ratio	ratio	Low	O	1.15	1.01	1.18	1.32	1.03	1.06
			L	.74	.81	.81	.77	.66	.76
		High	O	1.61	1.43	1.43	1.64	1.27	1.33
			L	.95	1.04	.93	1.02	.86	.88
Total weight	gm	Low	O	.142	.156	.129	.132	.178	.117
			L	.139	.177	.147	.131	.179	.125
		High	O	.203	.196	.163	.198	.253	.133
			L	.217	.228	.170	.168	.238	.148
Dead needle spirals	no.	Low	O	1.1	1.1	.8	1.3	1.1	.8
			L	1.4	1.1	1.3	1.6	1.8	1.3
		High	O	2.0	1.3	1.1	1.6	1.3	1.2
			L	2.3	2.0	1.7	2.7	2.4	2.0
Green needles	% (Estimated)	Low	O	24	28	6	20	31	8
			L	35	35	9	22	30	7
		High	O	63	77	35	41	81	63
			L	54	89	53	57	77	58

Table 33

F-values from analysis of variance of temperature and liming experiment (Expt. W). NS = not significant, * = significant at 5% level, ** = significant at 1% level.

Source of Variation	d.f.	CHARACTERISTIC Height	Root Length	Root Weight	Shoot Weight	Shoot-Root Ratio	Total Weight	# Dead "Whorls"	% Green Foliage
Source	1	4.82*	<1NS	1.76NS	<1NS	2.67NS	<1NS	3.63NS	<1NS
Species	2	22.63**	15.03**	18.47**	35.93**	3.46*	28.50**	11.17**	24.75**
Source X Species	2	6.20**	2.25NS	2.10NS	8.39**	3.54*	4.93**	<1NS	2.56NS
Trees/Source X Species	6	5.63**	2.06NS	3.76**	5.43**	<1NS	5.04**	2.95**	4.63**
Liming	1	17.78**	9.60**	11.73**	39.95**	170.65**	<1NS	49.58**	1.73NS
Temperature	1	<1NS	11.96**	78.89**	17.04**	60.58**	53.85**	47.83**	181.45**
Liming X Temp.	1	<1NS	<1NS	<1NS	<1NS	1.22NS	<1NS	5.64*	<1NS
Source X Environment	3	<1NS	<1NS	<1NS	<1NS	<1NS	<1NS	1.96NS	<1NS
Species X Environment	6	1.92NS	1.33NS	1.75NS	<1NS	<1NS	1.31NS	<1NS	1.59NS
Source X Species X Environment	6	<1NS	1.18NS	<1NS	<1NS	<1NS	<1NS	<1NS	1.32NS
(Trees/SXS) X Environment	18	<1NS	<1NS	5.89**	1.01NS	<1NS	<1NS	1.33NS	<1NS
Error	140								

increased height. Area 4 seedlings of P. rigida and P. virginiana were taller, and those of P. pungens, shorter, than those from Smith Mountain. P. rigida was generally shorter than the other species. Only P. rigida grown at high temperatures on limed soil was as tall as the other species.

Root length: Number of seedlings and height before treatment removed most of the root length variation. Species growth during treatment was not significantly different. Overall, P. pungens seedlings had the longest roots (26.1 cm) and P. virginiana the shortest (20.6 cm). Liming decreased root length (21.9 cm compared to 24.5), and temperature significantly increased it for area 4 seedlings.

Root weight: Root weight, after correction for seedling number and original height, differed by species, liming and temperature. Liming and low temperature decreased root weight. P. pungens was heavier than the other species, especially at Smith Mountain.

Shoot weight: Liming and temperature differences were not apparent after the variation associated with the covariates was removed. P. pungens is heavier than other species, especially for the Smith Mountain source, and P. rigida is heavier than P. virginiana.

Shoot/root ratio: Species differences were not significant. Liming and low temperatures cause less root

per shoot weight for all seedlings.

Total weight: No differences in total weight were found between treatments after initial height differences were accounted for. P. pungens is heavier than the other species, especially from Smith Mountain.

Number of dead needle spirals: This factor increased with liming and high temperature. P. rigida had the highest number (average 1.7) and decreased the most with lower temperature.

Color: Color interpretation differs somewhat depending on species. Seedlings from the sources of P. virginiana used seem to lose green color in winter normally, but the other species do not. Thus, loss of "greenness" by P. virginiana cannot really be compared with the other species. It usually turns a bright reddish purple, compared to a dull grayish purple for the other species in the experiment. Low temperature caused loss of green (21% green compared to 62% at high temperature). P. rigida is 20 to 35% green, on the average, for treatments at low temperature, and 41 to 63% at higher temperatures. P. pungens is 28 to 35% green at low, but 77 to 89% green at high temperatures, thus suffering a greater loss of healthy-appearing tissue at low temperatures.

Discussion. Variation within the species populations at a source (*i.e.* that due to "trees") is significant for 6 of 8 characteristics considered.

The low temperature treatment caused reduced root/shoot ratio, reduced total weight and reduced green coloring and dead needle whorls.

Generally, liming at these temperatures increased height, top weight and the number of dead needles. It decreased root weight and length, and root:shoot ratio. Its effects on root weights and root:shoot ratio were generally opposite those found in experiment C, which grew at outside temperature and light conditions.

Species differences were similar to those found in experiment C. No different responses of species to temperatures or liming were significant in total regressions or analysis of variance. The differential response of *P. pungens* and *P. rigida* color to temperature was not analyzed as such, but it appears that *P. pungens* is more affected by low temperature than *P. rigida*. Experimental conditions were such that no large differences occurred between species responses. A higher light intensity might have helped to cause such differences. If photosynthesis were less light-limited, temperature differences might have been more apparent.

Some differences between sources within species occurred. Within Pinus pungens, Smith Mountain plants were taller, but had a shorter and, in unlimed soils, a heavier root system. Liming increased height less and reduced RSR more in Smith Mountain than in area 4 seedlings. Virginia pine from Smith Mountain lost less green color, at least at high temperatures. Roots of area 4 seedlings were longer. Liming increased number of dead needles more in Smith Mountain than in area 4 seedlings. Pitch pine sources showed almost no differences.

Bud Formation and Growth Resumption of Seedlings

Bud formation and time at which experimental seedlings began growth was observed in 1967. Experiment D plants, outside since April, 1966, were moved into the greenhouse January 9-11, 1967. Plants were moved by replications, so all seed sources were treated alike, on the average. On January 28, terminal buds were scored as follows:

1 = no bud apparent.

2 = green bud-like structure with no scales.

3 = bud, scales poorly developed.

4 = well-formed bud, well-developed dark brown scales.

Each plant (20 per mother tree) was scored. Means and standard deviations of the rating are shown in Table 34. Pinus virginiana had less well developed buds than P. pungens or P. rigida. P. pungens showed no large differences, except that the most southern source had the least developed buds.

Experiment D seedlings were examined to determine which ones had begun terminal elongation, on February 19 and 25, March 3, 10, and 18, and April 1. Results are plotted in Fig. 28. Sources are numbered as in Table 34. The greenhouse was heated to a minimum temperature of 55 F at night and 70 F during the day. No lights were left on after sundown, but lights in neighboring greenhouses and incidental use of the lights at night may have caused an effective photoperiod longer than the natural one.

Pinus virginiana obviously began growth earlier than the other species. Areas 4 and 1 were ahead of the other sources of P. pungens. Although they are quite close to each other, area 1 is on Moore's Knob, a monadnock separated from the Blue Ridge, where area 4 is located. The areas have no common features suggesting a different behavior than the species from other areas.

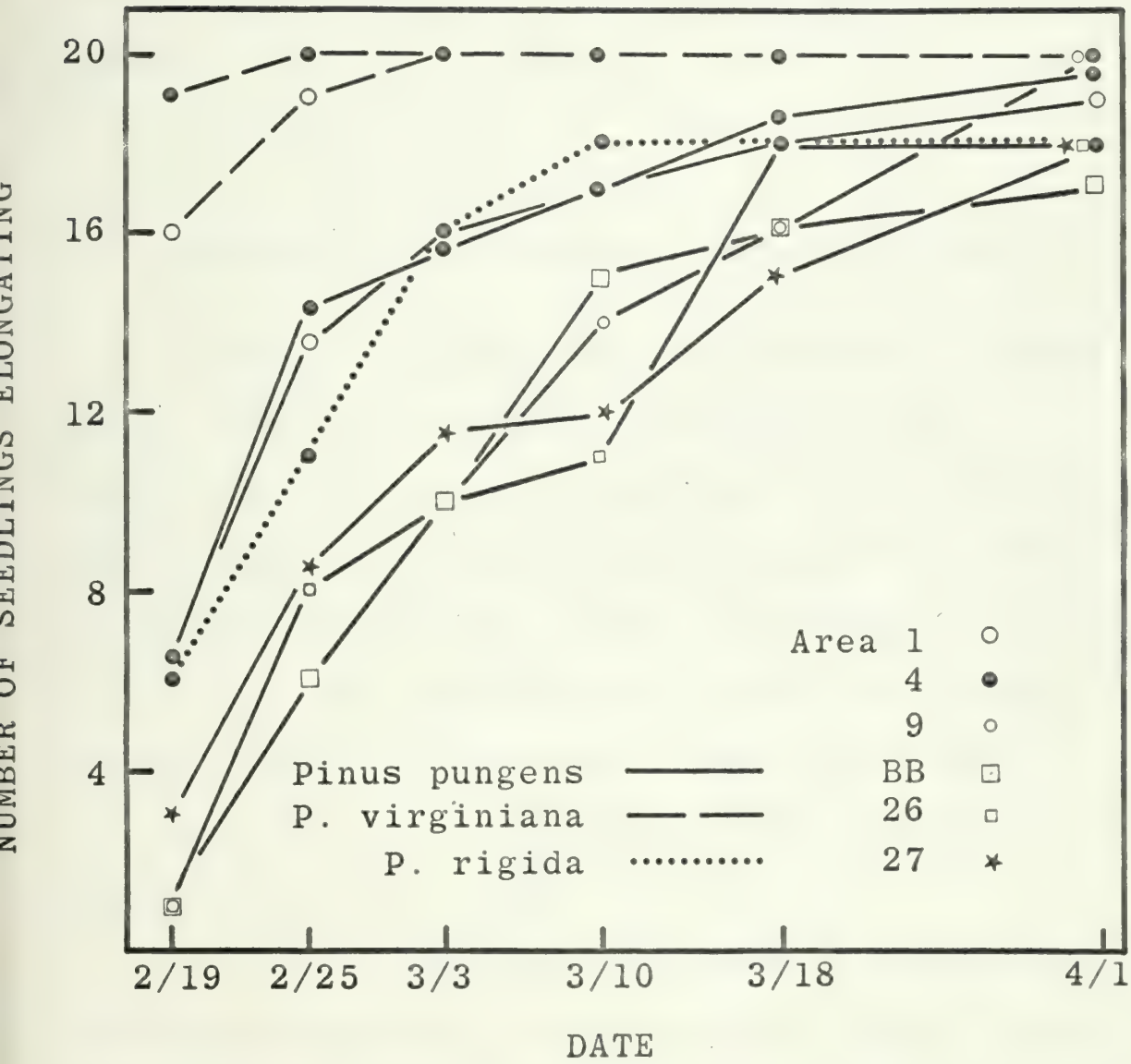
P. virginiana seedlings differed somewhat from the other species in bud set and growth resumption. Conditions were not controlled, so no statements regarding

Table 34

Condition of buds on experiment D seedlings with standard deviation of the rating (n = 20). 1 = no bud formation, 4 = best-developed buds. T = *Pinus pungens*, V = *P. virginiana*, P = *P. rigida*.

Source (Area. Tree Number)	Species	Latitude (degrees)	Elevation ft. (m)	Avg. bud rating
BB	T	34.5	2450 (747)	2.4 ± 1.3
9.2	T	36	3450 (1052)	3.6 ± 0.7
1.1	T	36.5	2415 (737)	3.4 ± 0.9
1.3	T			3.8 ± 0.5
1	V			1.9 ± 0.8
4.1	T	37	3220 (982)	3.3 ± 0.8
4.6	T			3.3 ± 0.9
4.7	T			2.8 ± 0.8
4	V			1.6 ± 0.6
4	P			3.3 ± 1.0
27.1	T	38	2900 (884)	3.5 ± 0.9
27.2	T			3.1 ± 1.1
26.4	T	40	400 (122)	3.5 ± 0.9

Figure 28. Number (of 20) of 1-year old seedlings resuming terminal growth by a given date. Data for *Pinus pungens* from area 4 are the means of seedlings from 3 trees; from areas 1 and 27, of those from 2 trees.


NUMBER OF SEEDLINGS ELONGATING
20
16
12
8
4
2/19
2/25
3/3
3/10
3/18
4/1
DATE
Pinus pungens
P. virginiana
P. rigida
Area 1
4
9
BB
26
27

the factors to which it responded differently can be made. P. virginiana appears able to take advantage of the favorable change in temperature more rapidly than P. pungens or P. rigida.

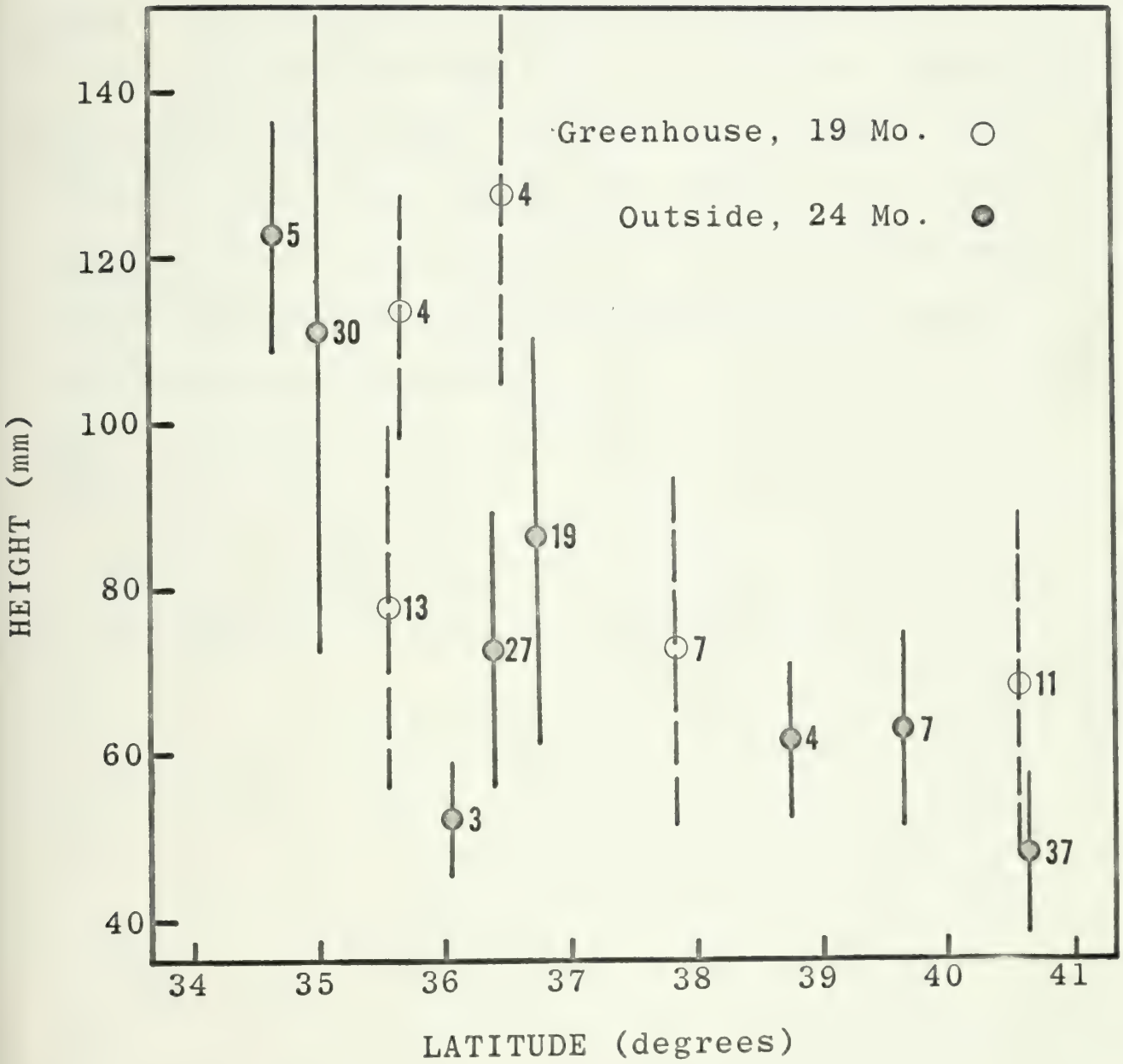
Seedling Height in Relation to Source Latitude

Seed of P. pungens from several sources was planted May 17, 1966, in 6-inch plastic pots in area I soil. Several plants per pot grew. Seedlings, left in the greenhouse, showed only one flush of growth during 1967. Time of bud break varied widely, but was not recorded. Seedlings of several sources, in similar pots and soil were planted January 29, 1966, but kept outside after May 13. Height of both groups, measured in January, 1968, is plotted over latitude of the source in Fig. 29.

Among the greenhouse-grown plants, a good relationship between height and latitude of origin exists. The one aberrant group, from about 36 N, is from 4300 feet elevation, over 1000 feet higher than the other sources in the group.

Plants grown outside showed a less direct relationship. The tallest sources were from northern and central Tennessee and the shortest from area 24, the same source as the shortest greenhouse-grown plants. A latitudinal

Figure 29. Height of seedlings grown in 6-inch plastic pots in area I soil, $\pm$ 1 standard deviation, as a function of latitude of seed origin. Number of seedlings in each mean shown beside means.


Greenhouse, 19 Mo.
Outside, 24 Mo.
HEIGHT (mm)
LATITUDE (degrees)
140
120
100
80
60
40
34
35
36
37
38
39
40
41
5
30
4
4
13
19
27
3
7
4
7
11
37

gradient in height growth of several provenances of *Pinus taeda* grown in northern Florida was found by Perry *et al*. (1966). Increased daylength supplied by floodlight removed only part of the variation that they found. Another study showed that cold-climate sources of *P. taeda* grew well only where they were local. Except in the coldest planting sites, sources from areas with higher rainfall and warmer winters grew fastest (Wells & Wakeley, 1966).

IX. DISCUSSION

This study has outlined some conditions associated with the sites where Pinus pungens occurs, and compared characteristics of the species with those of competing pines. Observations and experiments indicating the possible importance of several environmental factors and plant characteristics in determining the distribution of the species have been reported.

The use of single factors of the environment to explain the distribution of a plant species is condemned by Cain (1944: p. 18): "It is erroneous, then, to speak of a single factor as being limiting..." However, others treat the holocoenotic concept of the environment somewhat differently, recognizing the simultaneous interaction of all factors and the plant, while maintaining that a single factor may impose the ultimate limit of distribution at a given place and time (Billings, 1952; Mason & Stout, 1954). In the present discussion, the latter viewpoint will be accepted, and the place, time, and mode of action of factors

hypothesized to be limiting will be specified.

The limitations of the data upon which these discussions are based should be kept in mind. Many interspecific comparisons, especially those involving seedling physiology, are based on progeny from one or two trees from one or two areas. Plants were grown under conditions greatly differing from those in the field. Any physiological differences found can be, at best, suggestive of real differences. More sources and larger samples would be necessary to confirm them, and comparisons with observations of natural, seeded, or planted seedlings in the field should be made.

The Environment of Table Mountain Pine Stands

Pinus pungens stands occur most often on southwest-facing slopes, at the mid-elevations of the Appalachian Mountains and on outlying monadnocks. The species appears almost restricted to non-calcareous rocks, usually those on which exposed topographic situations develop. Soils are shallow, rocky, acid, and poor in nutrients. These sites are warmer and drier than those on other aspects, or those with less exposure or with deeper soils. Differences

in temperature and vapor pressure deficit between these stands and adjoining forests increase on the hotter and drier days.

Differences between Table Mountain pine stands and adjacent "oak" stands on shale are not the same as the differences between pine and oak stands which occur on other substrates. Pine stands have more "potential solar beam irradiation" than oak stands, in December in stands on shale but in June in non-shale stands. Pine stands on shale have less calcium, potassium, magnesium, and manganese in the topsoil than do oak stands on shale, and have less calcium and magnesium in the subsoil. Non-shale pine stands have less magnesium in topsoil and nitrate in the subsoil than oak stands. Soils formed from shale under pine stands have a lower pH than those under oak stands on shale.

Almost all Table Mountain pine stands sampled showed signs of one or more fires, as scars on trees, charcoal in the soil, burned bark, and charred logs. Patches of even-aged trees in many stands were probably the result of fire. The only recent burn seen (area 10) killed *Pinus pungens* and *P. rigida* on the top of a small lead, but did no damage in the draws on either side. Fire appears to be more frequent or damaging on sites occupied by Table Mountain pine than on adjacent areas.

The location of some stands containing Table Mountain pine, on the middle slopes of the mountains, corresponds with the location of the "thermal belts." A correlation between such mid-slope areas with higher minimum temperatures than on higher or lower slopes was found by Billings (1954) with the pinyon-juniper zone in western Nevada. This temperature inversion phenomenon causes a zone where frost frequency and duration are reduced, perhaps enough to allow the pine to survive, while it could not above or below. Inversions in North Carolina are most common and best developed in April, May, and November (Cox, 1923), periods when they would be of most benefit to P. pungens in terms of preventing frost damage to reproductive processes and young growth, and allowing early bud break and early-and late-season photosynthesis.

Differences in vegetation were also found between Table Mountain pine and oak stands. Quercus prinus, Carya spp., Cornus florida and Hamamelis virginiana were less important in pine than in oak stands, while Pinus rigida, P. virginiana, Q. ilicifolia, Gaylussacia baccata, Pteridium aquilinum and Tephrosia virginiana were more important in pine stands.

Since the environment of an area is best integrated by the natural vegetation present (Billings, 1952), known

characteristics of plants which were more important in a given type of stand may suggest which environmental differences between stands are most important. For example, Pteridium aquilinum, with higher importance rating in pine stands, is noted for its occurrence on burned areas (Clarkson, 1966), and is fire resistant due to deep rhizomes (Dansereau, 1957). However, it is susceptible to frost (Watt, 1950).

The Gaylussacia baccata-Vaccinium vacillans-V. angustifolium synusia, found intact or in part with many Table Mountain pine stands, is associated with acid, well-drained soils on Long Island, in areas which have considerable illumination (Reiners, 1965). This synusia is able to do well where frequent burning occurs.

"Habitat adaptation numbers" assigned to species for upland New Jersey (Buell et al., 1966; Davidson & Buell, 1967) indicate the types of sites on which these species are found. Species associated or more important with Pinus pungens stands (Table 12) were given the following numbers (1 = most xeric, 10 = most mesic): Pinus rigida, 1; Quercus coccinea, 2; Betula lenta, 5; Q. ilicifolia, 2.5; Gaylussacia baccata, 1; Pteridium aquilinum, 3.6. Species negatively associated with pine stands, or of less importance there, but present in neighboring stands, were assigned adaptation numbers as follows: Q. prinus, 2; Carya spp., 5; Cornus florida, 7;

Hamamelis virginiana, 8. Chestnut oak, although more important in oak stands, is also important in pine stands. Betula lenta, however, is not common in pine or oak stands, although it is more important in pine stands where it is present (Table 9). Species associated and dissociated with Table Mountain pine are usually those considered the more xerophytic, or more mesophytic, respectively, in the upland forests of New Jersey, supporting the contention that pine sites are more xeric than the nearby oak sites.

Areas supporting Table Mountain pine stands also differ in substratum conditions. Stands which appear to be most stable on non-shale areas occur with much rock outcrop and low topsoil magnesium. Permanent stands on shale are found on southern aspects, with shallow litter and on soils with low water-holding capacity. Permanent non-shale stands have less basal area of all species and also of Pinus pungens than do temporary stands, probably indicating they have less capacity to support vegetation.

Permanent stands on non-shale rocks were associated with Tephrosia virginiana, but Pinus rigida, P. strobus, Nyssa sylvatica, Castanea dentata, and Vaccinium angustifolium were dissociated or less important on them than on temporary ones. On shale, Quercus prinus was less important in permanent stands, and Amelanchier spp. were dissociated with

permanent stands.

Environmental Factors Limiting the Distribution of *Pinus pungens*

Low temperatures. That Table Mountain pine usually grows on warmer slopes suggests that low spring and winter temperatures may limit it. This is especially true in some shale-bank areas, where the species occurs only at the extreme upper levels on the east slopes, but much lower on the west slope. Although *Quercus prinus*, *Pinus virginiana* and other species are present, scattered over the east slope, the total cover is much less than on the west, and space is available for *P. pungens*, were it able to grow there.

Effects of low temperatures on seed germination and seedlings differed with species. Germination of seed of *Pinus pungens* reacts similarly to that of *P. virginiana* at the lower temperatures used. However, *P. rigida* seed germinated significantly over a wider range of temperatures than the other species. Time for young Table Mountain pine seedlings to develop increases and their root length decreases more, as soil temperature decreases, than that of Virginia pine seedlings. For seedlings three to six months

old, low temperatures caused reduced root weight and decreased root:shoot ratios, but no significant differences between species reaction to temperature were found. *Pinus pungens* did appear to lose green coloration more than *P. rigida*, under the cold temperature regime.

The effects of low temperatures and light intensities on seedling photosynthesis were not investigated. Comparisons of Table Mountain pine to competing pine and hardwood species, in regard to photosynthetic rates, should help support or disprove this hypothesis of limitation by these factors. A reduction by low temperature and light intensity of Table Mountain pine photosynthesis during the cool seasons might limit the species severely on north and east slopes, compared to the warmer, sunnier slopes. Conditions would probably be quite suitable for seedling photosynthesis on areas with considerable direct insolation, on some winter days. Even if there is some breakdown of chloroplasts as found with some species, winter photosynthesis might be considerable (Fritts, 1966). That *P. virginiana* seemed to rely to a greater extent on primary needles, probably more efficient at low light intensities (Bormann, 1958), may give it some advantage on the less insolated slopes.

Lower temperatures and lower light intensities on north slopes may also cause hardship to older Table Mountain

pines, by reducing cold-season photosynthesis. If these plants have low intrinsic rates of photosynthesis, this reduction might cause the plant to be less efficient in maintaining necessary photosynthetic surface or root growth.

Pinus pungens, by "flowering" and initiating twig growth earlier, is more liable to frost damage than the other pine species. In the colder year during which phenology was observed, P. pungens reached 50% twig elongation an average of 8.4 days later than in the warmer year, compared to 14 days later for the other pines. This suggests that it may respond less to year-to-year temperature differences. Early pollen release of Table Mountain pine appeared at all areas observed. Should establishment and growth occur in areas with late frosts, reproduction is likely to be disrupted. Similar northern range limitation of the early-flowering P. radiata has been suggested (G. L. Stebbins, in discussion following Bannister, 1965).

High temperatures. A possible effect of higher temperatures at lower elevations, as on the Piedmont, could be to prevent cone serotiny. This removes a major advantage the species has over the other pines after fire. Lower elevation stands in the northern part of the range have mostly non-serotinous cones, although these may have resulted from the extended drought in the region for several years

preceding collections.

Excess moisture. *Pinus pungens* is normally a plant of dry sites. Excessive moisture on slopes with less evaporation, especially in winter, might injure the root system. Indications of adverse effects of saturated soil were shown by some seedlings in the greenhouse. However, *P. pungens* does grow in some damp areas and around at least two high elevation bogs. Excess moisture alone may not be a problem for it, if other circumstances are favorable.

Soil chemistry. Much of the difference between soil nutrient levels might be due to differences in absorption and cycling by the vegetation. However, some real differences seem to be present in the subsoils.

Liming to 1200-1500 lb/acre (1104-1380 kg/ha) of calcium and 170-240 lb/acre (156-221 kg/ha) of magnesium increased most measures of growth for the three pine species used. It had no obvious adverse effects on *P. pungens* by itself. Absence of *P. pungens* from limestone may be related largely to the general correlation of limestone with valley topography in the range of the species.

Biotic factors. Effects of squirrels and insects on seed crops, growth, and tree form are straight-forward.

Squirrels may limit the growth rate and competitive ability of P. pungens by destroying past growth and photosynthetic tissue, as well as limiting the reserve seed crop.

Mycorrhizal relations may limit the species range. Should it be able to form mycorrhizae with fewer fungi, or with fungi with more narrow tolerances than other pines, its range might be limited by that of the fungi. In Pinus virginiana in unfumigated soil in Experiment C, the number of mycorrhizae increased more with liming than in P. pungens. In P. rigida, the relative numbers of different types of mycorrhizae present changed. Numbers and types of mycorrhizae on Table Mountain pine changed only slightly with liming. It appeared less able to respond to the absence of mycorrhizae, also, although no statistical differences support this. Pinus pungens without mycorrhizae had a relatively smaller increase in root:shoot ratio over those with mycorrhizae, than the other species.

An effect not considered previously may limit distribution of Table Mountain pine and the other pines. Damping-off of seedlings occurred in a group of seedlings planted in greenhouse soil, destroying most of the seedlings despite fungicidal treatment. However, no seedlings grown in area I soil were lost. Although damping-off of conifer seedlings is caused by a variety of fungi, and thus may occur under many circumstances, it is usually most

destructive under certain conditions. Weakly acid or neutral soils, high nitrogen levels, low light intensities, and excess moisture have been found to favor the disease in forest nurseries (Boyce, 1961: p. 84-87). These are conditions not associated with P. pungens which might cause its exclusion by allowing damping off. If differences in species susceptibilities existed, distribution of the pines could be affected. Apparently little if any work on the effects of damping-off on natural regeneration has been done. Illick & Aughanbaugh (1930) propose that it excludes P. rigida from areas of calcareous soil in Pennsylvania, however. Similar exclusion of P. pungens appears possible.

Effects of other vascular plants are probably very important in determining the distribution of Pinus pungens. It occurs on areas least favorable for rapid plant growth, from which some species common on neighboring areas are usually excluded. These conditions may limit the possible rate of growth of Table Mountain pine less than that of other species, making its rate of development fast enough to compete successfully for minerals, or water, or canopy space. These conditions probably limit ultimate size of the pine less than that of the other species, allowing continued successful competition, not possible on more

fertile areas where hardwoods eventually outgrow the pine.

Conditions on Table Mountain pine sites are not conducive to good growth of trees of many hardwood species. Severe drought was observed to kill trees of several species of southern Appalachian oaks (but not Quercus prinus) without injuring the pines present (Hursh & Haasis, 1931). The lack of litter cover in some stands would not favor oak or hickory establishment (Barrett, 1931; Fowells, 1965). Site index of Q. coccinea and Q. velutina measured near Asheville, North Carolina (Doolittle, 1957), increases with depth of the A horizon of the soil and decreases from lower to upper slopes. It is quite low on Porters and Ashe soil series, associated with Pinus pungens in several areas, and is lowest on west and southwest aspects and on mor humus types. These conditions associated with poor oak growth are those generally characterizing Table Mountain pine sites.

Allelopathic effects from species competing with Table Mountain pine, should they exist, are probably reduced on sites where plant density and vigor are limited. Inhibitory effects of several species (including Gaultheria procumbens, present in a third of sampled stands) on seed germination of Pinus banksiana have been shown (Brown, 1967).

Pinus rigida and P. virginiana are generally intolerant of shade, and observations in the field indicate

that P. pungens is probably as intolerant or more so. Almost no seedlings of P. pungens occur on sites without exposed mineral soil or with a dense canopy or shrub layer.

Characteristics Adapting Pinus pungens to Its Habitat

Differences in morphology and physiology which contribute to different distributions have been demonstrated in several pine species. Pinus edulis in northern Arizona survives at warmer, drier, lower elevations than P. ponderosa because its larger seed produces seedlings with a relatively longer root, which are more drought resistant than the other species (Rand, 1965). On a southern California mountain range, low elevation P. attenuata and P. coulteri seedlings develop deeper root systems than P. lambertiana, which is restricted to high elevations (Wright, 1966).

Pinus pungens has some adaptations paralleling those of the lower elevation western pines cited above (i.e. those of the drier habitats). Larger seeds of Table Mountain pine produce larger seedlings with longer roots than competing species, at least under experimental conditions. Experimental evidence suggests that young P. pungens seedlings may lose less water than P. rigida. Natural root depth was not closely examined, however. Rocky soils, often closely

underlain by bedrock, make excavation difficult. Roots probably extend down through cracks in the bedrock.

The usual needle number in Pinus rigida is three, compared to two in P. pungens and P. virginiana. Dividing a given volume of needle into thirds would increase the surface-to-volume ratio of a fascicle by a factor of $(2\pi + 3)/(2\pi + 2)$, or 1.12, over that with two needles. Stomata are present on all surfaces of hard-pine needles (Harlow, 1931). Assuming equal stomatal density and behavior, and equal cuticle on both types, gas exchange and water vapor loss would be higher in the three-needle fascicles. This would be favorable unless water loss were a major factor limiting survival and growth. Needle number suggests that Pinus rigida would be less likely to survive in the most extreme areas, in terms of transpiration stress and water supply, than either of the two-needled pines. Observations more or less fit what would be expected from the above discussion, since pitch pine tends to be peripheral on extreme sites where the other species occur throughout.

Leaders and twigs of Pinus pungens elongate and the species produces pollen earlier than associated pine species. Thus, it avoids the maximum amount of evaporative stress during the period of elongation, when it may be most sensitive to drying, as found for P. cembra (Tranquillini, 1965).

Fire has a profound effect on the maintenance and characteristics of pine forests. Pinus insularis forests in Luzon, Philippines, are almost entirely a result of human disturbance and the accompanying fires (Kowal, 1966), as are those in many other tropical, as well as temperate, regions.

In the New Jersey pine region, fire frequency and severity determine the composition and size of the vegetation. Repeated fires result in stands lacking Pinus echinata and the arborescent oaks, which produce seed only after about 20 years. Early-seeding pitch pine and Quercus ilicifolia sprouts become dominant (Little, 1964). The pine forests of the southeastern U.S. Coastal Plain are maintained in a similar way by fire, and Pinus contorta is successional after fire in the upper P. ponderosa, the Douglas-fir, and the subalpine spruce-fir zones of the Rocky Mountains (Oosting, 1956). Wright (1966) found P. attenuata only on areas burned in about the last 60 years in the San Bernardino Mountains of California.

Serotiny appears to be an adaptation to repeated fires. Pinus rigida is serotinous in some areas where fire is very common (Fowells, 1965). In the Rocky Mountains, P. contorta has reflexed, serotinous cones, much different from those in the Sierra Nevada, where fire is not so important in its ecology (Critchfield, 1957). Cones of

P. serotina, P. banksiana, and P. attenuata, associated with burned areas, are serotinous. The latter two species have reflexed, assymetrical cones with thick scales on the side away from the branch (Fowells, 1965; Sargent, 1897). Pinus pungens, being generally serotinous, has a reproductive advantage over the non-serotinous P. rigida and P. virginiana with which it occurs. Its serotinous cones and association with burned areas appear similar to the situation of Pinus attenuata in the western United States.

Bark thickness of species also differs. Pinus rigida develops thick bark early and is quite fire resistant, in contrast to the thin-barked P. virginiana (Illick & Aughanbaugh, 1930; Slocum & Miller, 1953). Pinus pungens bark is considerably thicker than that of the fire-susceptible P. virginiana, although thinner than that of P. rigida, at least on trees up to 15 inches DBH. Nothing is known about thermal properties of the bark which would also affect susceptibility to fire damage.

Dormant buds along the bole and branches of P. rigida which allow recovery from defoliation are absent in P. pungens and P. virginiana (Stone & Stone, 1943). Pinus rigida has more basal buds which sprout after injury, allowing recovery of fire-and animal-damaged young trees, than the other species. Those buds in P. virginiana usually

elongate the second year (Stone & Stone, 1954) and its sprout growth is uncommon and not usually persistent (Fowells, 1965; Fenton & Bond, 1964).

The development of a basal crook in seedlings of pitch and shortleaf pines may protect the basal buds against fire (Little & Mergen, 1966). Pinus virginiana lacks this basal crook (Fenton & Bond, 1964). No report of such a crook in P. pungens was found, but the natural seedlings of P. pungens which were uprooted usually had a crook just above or just below ground level.

Fire aids reproduction of Table Mountain pine in several ways. It destroys litter, exposing mineral soil, and eliminates competing vegetation, allowing pine seedlings more light and water, and minimizing any allelopathic effects. It increases the rate of mineral cycling, important on sterile soils. Since litter favors establishment of oaks and hickories, repeated fires would minimize their reproduction.

Pinus pungens is better adapted to colonizing burned areas than the two competing pines, and better adapted to surviving fires than, at least, P. virginiana. It is better adapted to dry sites than P. rigida. Its phenology allows Table Mountain pine an advantage over both competing pines where spring temperatures are highest and spring frosts least likely.

Variation within Table Mountain Pine

Variation occurs along both latitudinal and elevational gradients, and some evidence for differences between physiographic regions appears. The strongest trends are along the elevational gradient.

Much of the variation measured within the species was from tree to tree. However, some regional differences were found. Needles are more slender (have a higher length: width ratio) in the south than in the north. Since elevation and latitude of sampling areas are negatively correlated, the effect of latitude may result from elevational differences. Cones from the north may have slightly fewer scales. Seed weight generally decreases with elevation.

Some physiological differences were found within *Pinus pungens*. In two comparisons of germination response to temperature, Blue Ridge sources had germination value curves displaced toward the warmer end than the Valley-and-Ridge sources. In a comparison of germination of seed from Pennsylvania, Virginia, and Georgia sources, the southern one responded most to higher temperature. Transpiration rates for northern seedlings were higher at 6 and 18 months of age, especially at higher soil moisture contents.

Young seedlings from Smith Mountain, a southern Virginia monadnock, develop more slowly than those from the Blue Ridge at the same latitude. The same sources, used in a temperature and liming experiment, showed a number of differences. Seed from Smith Mountain is heavier, and seedlings are taller, have a heavier root system, and show different reactions to liming than the Blue Ridge source. Liming caused less height increase and more reduction in root:shoot ratio than in Blue Ridge plants. Characteristics allowing rapid establishment and maximal chance for survival of young seedlings appear to be better developed at Smith Mountain. This area is about 1500 to 2000 feet (458-610 m) lower, and is warmer, and has somewhat lower soil nutrient levels than the Blue Ridge area. This differentiation must have occurred since the separation of these two populations, about 45 miles (72 kilometers) apart, which may have been more or less continuous during glacial times. The two populations appear to be ecotypes, developed in response to the different conditions in their separated habitats. Differences also exist between seedlings of *P. virginiana* and *P. rigida* from the two areas, although not so pronounced as those of *P. pungens*.

Height of seedlings from several sources varies inversely with latitude. Buds were less well-formed by a

Georgia source than others, and differences in the time seedlings took to resume growth in the greenhouse differed, although in no easily explainable pattern.

Conclusions

Pinus pungens appears to be confined to the warmest sites in the Appalachian Mountains by the effects of low temperature, including late spring frosts. Its restriction to the driest, most sterile habitats on these warmer slopes appears to be a result of minimal interference on these areas by other vegetation, and to its adaptation to the warm, dry conditions prevailing there.

Fire, most likely on dry, exposed sites, contributes to maintenance of Table Mountain pine stands by destroying the litter layer and hastening mineral cycling, opening the canopy, releasing pine seed, and killing much of the competing vegetation, at least back to ground level. Among competing pines, *P. rigida* appears to be less drought resistant than *P. pungens* while *P. virginiana* is more susceptible to damage by fire.

Without fire and man-made disturbances, *Pinus pungens* probably would exist only on extremely dry and sterile rock outcrops and steep shale slopes, where maximum

canopy would be quite open and litter cover would never remain complete. F. A. Michaux's early statement (1819) that fire and the effects of settlement would soon cause the extinction of P. pungens was overly pessimistic. These factors appear to allow it a wider distribution and greater abundance, rather than destroying the species.

X. SUMMARY

1. The Appalachian endemic, Pinus pungens (Table Mountain pine), occurs in small stands in the mountains from central Pennsylvania to northeastern Georgia, usually at elevations of 1000 to 4000 feet (305 to 1220 m). Stands on the Piedmont from New Jersey to Georgia are usually associated with monadnocks or are near major rivers

2. Twenty-nine Table Mountain pine stands were sampled in 1965, and the results used as a basis for later work. Stands of the species, and neighboring stands without it, were sampled in 1966 in 19 areas throughout the range. Samples of needles, cones, soil, and rock; increment cores; and data on the vegetation, topography, and microclimate were taken.

3. Table Mountain pine stands usually occur on southern to western aspects on areas with thin, rocky soil. In the Valley-and-Ridge province, these stands are often on shaly slopes and ridges. Soils under Table Mountain pine

stands have lower nutrient levels and lower pH than under adjoining stands, both in topsoils and subsoils. Higher spring and summer temperatures and higher vapor pressure deficits were measured in Table Mountain pine stands than in the adjacent forests; the difference increased on the hotter and drier days.

4. Those Table Mountain pine stands appearing to be permanent were associated with shallower litter, more rock outcrop, and had less basal area, than more obviously successional ones.

5. Table Mountain pine occurs most often with wide-ranging species such as Quercus prinus, Q. coccinea, Pinus rigida, P. virginiana, Kalmia latifolia, Vaccinium vacillans (including V. pallidum), V. stamineum, V. angustifolium, Gaylussacia baccata, Smilax spp., and Pteridium aquilinum. Many of these species are favored by fire or are considered drought-tolerant.

6. Squirrels (probably Tamiasciurus hudsonicus) eat seed stored in the serotinous cones, and, by cutting branches to get the cones, destroy photosynthetic surface and past growth.

7. Fire aids the reproduction of Pinus pungens by destroying competing vegetation and litter cover, while releasing seed from the pine's serotinous cones. Table

Mountain pine appears to be more fire-resistant than most competing species.

8. Cone length, width, and length:width ratio, and seed weight, of Table Mountain pine decrease with elevation. Length:width ratio of needles collected in natural stands is higher south of 37° N than farther north. Experimental seedlings from northern sources have higher transpiration rates, at least at higher soil water contents.

9. Adaptations of *Pinus pungens* to warm, dry sites include larger seeds, which result in heavier seedlings with longer root systems, more lateral roots, and more branches than those of *P. rigida* and *P. virginiana* grown under the same experimental conditions. Very young seedlings have a longer root and those 5 to 6 months old have lower transpiration rates, than seedlings of *Pinus rigida*. Seedlings of *P. pungens* develop mature needle fascicles earlier than young plants of *P. virginiana*. Table Mountain pine sheds pollen about two weeks earlier than *P. virginiana* and three to four weeks before *P. rigida*. Twig elongation, seedling height growth, and needle elongation in the field were also earlier than in the other pine species, at least during the colder year of measurement (1966). Early activity allows growth processes to occur during time of least drought stress.

10. Addition of calcium and magnesium to experimental soils had no clearcut adverse effects on Table Mountain pine seedlings.

11. Seeds of *Pinus pungens* germinated over a narrower temperature range than did those of *P. rigida*. Root length of very young seedlings was reduced more at high and low temperatures than that of *P. virginiana*.

12. Table Mountain pine appears to be limited by low temperatures or late frosts on slope aspects other than southwest, at higher elevations, and to the north and northwest, because of injury to new growth or to reproductive processes. Interference by other species probably excludes it from many areas it could occupy. Warmer temperatures at lower elevations may decrease the incidence of cone serotiny, thus removing a major advantage over competing species. Increased fire protection and a decrease in land abandonment have apparently reduced the establishment of new stands during recent years and will probably further reduce establishment in the future.

13. Detailed field studies of root habits, of water potentials during droughts, and of survival and growth of planted, seeded, or natural seedlings on different aspects, along with further phenological studies and analysis of photosynthetic patterns and rates of the pine are needed

before the ecological situation of *Pinus pungens* can be clearly understood.

LITERATURE CITED

XI. LITERATURE CITED

Allard, H.A. 1946. Shale barren associations on Massanutten Mountain, Virginia. Castanea 11: 71-124.

_____ and E.C. Leonard. 1943. The vegetation and floristics of Bull Run Mountain, Virginia. Castanea 8: 1-64.

_____ and _____. 1952. The Canaan and the Stony River Valleys of West Virginia, their former magnificent spruce forests, their vegetation and floristics today. Castanea 17: 1-60.

Allen, R.M. 1963 Geology and mineral resources of Greene and Madison Counties. Virginia Div. Mineral Resources Bull. 78. 102 p.

Bannister, M.H. 1965. Variation in the breeding system of Pinus radiata, p. 353-374. In Baker, H.G., and G.L. Stebbins (ed.) The genetics of colonizing species. Academic Press, New York.

Barbour, M.G., and C.H. Racine. 1967. Construction and performance of a temperature-gradient bar and chamber. Ecology 48: 861-863.

Barrett, L.I. 1931. Influence of forest litter on the germination and early survival of chestnut oak, Quercus montana, Willd. Ecology 12: 476-484.

Barrs, H.D. 1965. Comparison of water potentials in leaves as measured by two types of thermocouple psychrometer. Australian J. Biol. Sci. 18: 36-52.

_____. 1966. Root pressure and leaf water potential. Science 152: 1266-1268.

Best, G.N. 1886. Pinus pungens in New Jersey. Torrey Bot. Club Bull. 13: 126-128.

Billings, W.D. 1952. The environmental complex in relation to plant growth and distribution. Quart. Rev. Biol. 27: 251-265.

_____. 1954. Temperature inversions in the pinyon-juniper zone of a Nevada mountain range. Butler Univ. Bot. Stud. 11: 112-118.

_____. 1957. Physiological ecology. Annu. Rev. Plant Physiol. 8: 375-392.

_____, E.E.C. Clebsch, and H.A. Mooney. 1968. A low temperature plant growth chamber. Unpubl. Manuscript. 5 p.

Bormann, F.H. 1958. The relationships of ontogenetic development and environmental modification to photosynthesis in Pinus taeda seedlings, Ch. 10. In Thimann, K.V. (ed.) The physiology of forest trees. Ronald Press, New York.

Bouyoucos, G.J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Sci. 42: 225-230.

Boyce, J.S. 1961. Forest pathology. 3rd ed. McGraw-Hill Book Co., New York. 572 p.

Boyer, J.S. 1965. Effects of osmotic water stress on metabolic rates of cotton plants with open stomata. Plant Physiol. 40: 229-234.

_____ and E.B. Knipling. 1965. Isopiestic technique for measuring leaf water potentials with a thermocouple psychrometer. Proc. Nat. Acad. Sci. 54: 1044-1051.

Brent, W.B. 1960. Geology and mineral resources of Rockingham County. Virginia Div. Mineral Resources Bull. 76. 174 p.

Brown, R.T. 1967. Influence of naturally occurring compounds on germination and growth of jack pine. Ecology 48: 542-546.

Bryant, B. 1962. Geology of the Linville Quadrangle, North Carolina-Tennessee: A preliminary report. U.S. Geol. Surv. Bull. 1121-D. 30 p.

Buell, M.F., A.N. Langford, D.W. Davidson, and L.F. Ohmann. 1966. The upland forest continuum in northern New Jersey. Ecology 47: 416-432.

Cain, S.A. 1931. Ecological studies of the vegetation of the Great Smoky Mountains of North Carolina and Tennessee. I. Soil reaction and plant distribution. Bot. Gaz. 91: 22-41.

_____. 1944. Foundations of plant geography. Harper and Brothers, New York. 556 p.

Campbell, T.E. 1955. Freeze damages shortleaf pine flowers. J. Forestry 53: 452.

Chapman, A.G. 1941. Tolerance of shortleaf pine seedlings for some variations in soluble calcium and H-ion concentration. Plant Physiol. 16: 313-326.

Clarkson, R.B. 1966. The vascular flora of the Monongahela National Forest, West Virginia. Castanea 31: 1-119.

Coker, W.C., and H.R. Totten. 1945. Trees of the southeastern states. Univ. North Carolina Press, Chapel Hill. 419 p.

Collins, H.H., Jr. 1959. Complete field guide to American wildlife: East, central and north. Harper and Row, New York. 683 p.

Cooperrider, T.S., and R.F. Thorne. 1964. The flora of Giles County, Virginia. II. Castanea 29: 46-70.

Cox, H.J. 1923. Thermal belts and fruit growing in North Carolina. Monthly Weather Rev. Suppl. 19. 106 p.

Critchfield, W.B. 1957. Geographic variation in Pinus contorta. Maria Moors Cabot Found. Pub. 3. 118 p.

_____. 1963. Hybridization of the southern pines in California, p. 40-48. In Proc. Forest Genet. Workshop, Macon, Georgia, October 25-27, 1962. Southern Forest Tree Improvement Comm. Sponsored Pub. 22.

Critchfield, W.B., and E.L. Little, Jr. 1966. Geographic distribution of the pines of the world. U.S. Dep. Agr. Misc. Pub. 991. 97 p.

Czabator, F.J. 1962. Germination value: An index combining speed and completeness of pine seed germination. Forest Sci. 8: 386-396.

Dallimore, W., and A.B. Jackson. 1954. A handbook of the Coniferae. Edw. Arnold, Ltd., London. 686 p.

Dansereau, P. 1957. Biogeography. Ronald Press, New York. 394 p.

Davidson, D.W., and M.F. Buell. 1967. Shrub and herb continua of upland forests of northern New Jersey. Amer. Midland Natur. 77: 371-389.

Davis, J.H., Jr. 1930. Vegetation of the Black Mountains of North Carolina: An ecological study. J. Elisha Mitchell Sci. Soc. 45: 291-318.

Daubenmire, R.F. 1943. Soil temperature versus drought as a factor in determining lower altitudinal limits of trees in the Rocky Mountains. Bot. Gaz. 105: 1-13.

Deen, J.L. 1937. Silvical characteristics of American trees. Brownell Photo-lithograph Co., Philadelphia. 99 p.

Dickey, S.S. 1926. The Table-Mountain pine. Nature Mag. 8: 38.

Dixon, D. 1961. These are the champs. Part II. Amer. Forests 67(2): 41-47.

Doolittle, W.T. 1957. Site index of scarlet and black oak in relation to southern Appalachian soil and topography. Forest Sci. 3: 114-124.

Dorman, K.W. and J.C. Barber. 1956. Time of flowering and seed ripening in southern pines. Southeastern Forest Exp. Sta., Sta. Paper 72. 15 p.

Duffield, J.W. 1951. Interrelationships of the Californian closed-cone pines with special reference to Pinus muricata Don. Ph.D. Thesis, Univ. California, Berkeley.

Duffield, J.W. 1952. Relationships and species hybridization in the genus Pinus. Z. Forstgenet. Forstpflanzenzuchtung 1: 93-97.

Fenneman, N.M. 1938. Physiography of eastern United States. McGraw-Hill Book Co., New York. 714 p.

_____ and D.W. Johnson. 1946. Physical divisions of the United States. U.S. Dep. Interior, Geol. Surv. (Map).

Fenton, R.H., and A.R. Bond. 1964. The silvics and silviculture of Virginia pine in southern Maryland. Northeastern Forest Exp. Sta., U.S. Forest Service Res. Paper NE-27. 36 p.

Fernald, M.L. 1950. Gray's manual of botany. 8th Ed. American Book Co., New York. 1632 p.

Fisher, P.L. 1941. Germination reduction and radicle decay of conifers caused by certain fungi. J. Agr. Res. 62: 87-95.

Flint, R.F. 1957. Glacial and Pleistocene geology. Wiley & Sons, New York. 553 p.

Forde, Margot B. 1964a. Variation in natural populations of Pinus radiata in California. Part III. Cone characters. New Zeal. J. Bot. 2: 459-485.

_____. 1964b. Variation in natural populations of Pinus radiata in California. Part IV. Discussion. New Zeal. J. Bot. 2: 486-501.

Forest Service Tree Name Committee. 1940. Approved changes in Sudworth's check list. U.S. Dep. Agr., Forest Service. 86 p.

Fowells, H.A. (ed.). 1965. Silvics of forest trees of the United States. U.S. Dep. Agr., Agr. Handbook 271. 762 p.

Frank, E.C. and R. Lee. 1966. Potential solar beam irradiation on slopes: Tables for 30° to 50° latitude. Rocky Mountain Forest and Range Exp. Sta., U.S. Forest Service Res. Paper RM-18. 116 p.

Freeland, R.O. 1952. Effect of age of leaves upon the rate of photosynthesis in some conifers. Plant Physiol. 27: 685-690.

Freer, R.B. 1950. A preliminary checklist of plants of the central Virginia Blue Ridge. Castanea 15: 1-37.

Fritts, H.C. 1966. Growth-rings of trees. Their correlation with climate. Science 154: 973-979.

Garman, H. 1913. The woody plants of Kentucky. Kentucky Agr. Exp. Sta. Bull. 169. 62 p.

Geiger, R. 1965. The climate near the ground. Harvard Univ. Press, Cambridge, Mass. 611 p.

Gerloff, G.C., D.G. Moore and J.T. Curtis. 1966. Selective absorption of mineral elements by native plants of Wisconsin. Plant and Soil 25: 393-405.

Gifford, C.L., and R. Whitebread. 1951. Mammal survey of south central Pennsylvania. Pennsylvania Game Comm., Harrisburg. Final Rep., Pittman-Robertson Project 38-R. 75 p.

Goebel, K. 1900. Organography of plants. Part 1: General organography. Transl. I.B. Balfour. Clarendon Press, Oxford. 270 p.

Golley, F.B. 1962. Mammals of Georgia, a study of their distribution and functional role in the ecosystem. Univ. Georgia Press, Athens. 218 p.

Griffin, J.R. 1965. Digger pine seedling response to serpentinite and non-serpentinite soil. Ecology 46: 801-807.

Grimm, W.C. 1950. The trees of Pennsylvania. Stackpole and Heck, New York. 363 p.

Haasis, F.W., and A.C. Thrupp. 1931. Temperature relations of lodgepole-pine seed germination. Ecology 12: 728-744.

Hack, J.T., and J.C. Goodlett. 1960. Geomorphology and forest ecology of a mountain region in the central Appalachians. U.S. Geol. Surv. Prof. Paper 347. 66 p.

Hadley, J.B., and R. Goldsmith. 1963. Geology of the eastern Great Smoky Mountains, North Carolina and Tennessee. U.S. Geol. Surv., Prof. Paper 349-B.

Haller, J.R. 1962. Variation and hybridization in ponderosa and Jeffrey pines. Univ. Calif. Pub. Bot. 34: 123-166.

_____. 1965. The role of 2-needle fascicles in the adaptation and evolution of ponderosa pine. Brittonia 17: 354-382.

Hardy, A.V. 1964. Low temperature probabilities in North Carolina. North Carolina Agr. Exp. Sta. Bull. 423. 43 p.

Harley, J.L. 1965. Mycorrhiza, p. 218-230 In Ecology of soil-borne plant pathogens. Univ. Calif. Press, Berkeley.

Harlow, W.M. 1931. The identification of the pines of the United States, native and introduced, by needle structure. New York State Coll. Forestry Tech. Pub. 32.

Harper, R.M. 1901. On a collection of plants made in Georgia in the summer of 1900. Torrey Bot. Club Bull. 28: 454-484.

Harper, R.M. 1967. Studying the Georgia flora and some red-letter days in the life of a botanist. Castanea 32: 1-17.

Hough, R.B. 1924. Handbook of the trees of the northern states and Canada. 3rd ed. Romeyn B. Hough Co., Lowville, N.Y. 470 p.

Hursh, C.R., and F.W. Haasis. 1931. Effects of 1925 summer drought on southern Appalachian hardwoods. Ecology 12: 380-386.

Illick, J.S. 1928. Pennsylvania trees. Pennsylvania Dep. Forests and Waters. 235 p.

_____ and J.E. Aughanbaugh. 1930. Pitch pine in Pennsylvania. Pennsylvania Dep. Forests and Waters Res. Bull. 2. 108 p.

Kaufmann, M. 1967. Water relations of pine seedlings in relation to root and shoot growth. Ph.D. Diss., Duke Univ. 147 p.

Keever, Catherine, H.J. Oosting and L.E. Anderson. 1951. Plant succession on exposed granite of Rocky Face Mountain, Alexander County, North Carolina. Torrey Bot. Club Bull. 78: 401-421.

Keith, A. 1894. Geology of the Catoctin Belt, p. 285-395 In 14th Annu. Rep. U.S. Geol. Surv., 1892-1893. Part II.

Kelley, A.P. 1931. Occurrence of Pinus pungens Lamb. on the Atlantic coastal plain. Torreya 31: 8.

King, P.B., and H.W. Ferguson. 1960. Geology of northeasternmost Tennessee. U.S. Geol. Surv. Prof. Paper 311. 136 p.

Knipling, E.B. 1966. Comparison of the dye method with the thermocouple psychrometer for measuring leaf water potentials. Ph.D. Diss., Duke Univ. 121 p.

Knopf, Eleanora B., and Anna I. Jonas. 1929. Geology of the McCall's Ferry-Quarryville district, Pennsylvania. U.S. Geol. Surv. Bull. 799. 156 p.

Komarek, E.V. 1966. The meteorological basis for fire ecology. Proc. 5th Annu. Tall Timbers Fire Ecol. Conf.: 85-125.

Kormanik, P.P., and E.L. Little, Jr. n.d. Trees and shrubs of the Lee Experimental Forest, Buckingham County, Virginia. Southeastern Forest Exp. Sta. 12 p.

Kowal, N.E. 1966. Shifting cultivation, fire, and pine forest in the Cordillera Central, Luzon, Philippines. Ecol. Monogr. 36: 389-419.

Kramer, P.J., and T.T. Kozlowski. 1960. Physiology of trees. McGraw-Hill Book Co., New York. 642 p.

_____, E.B. Knipling and L.N. Miller. 1966. Terminology of cell-water relations. Science 153: 889-890.

Kruckeberg, A.R. 1967. Ecotypic response to ultramafic soils by some plant species of northwestern United States. Brittonia 19: 133-151.

Krugman, S.L. 1966. Freezing spring temperatures damage knobcone pine conelets. Pacific Southwest Forest and Range Exp. Sta., U.S. Forest Service Res. Paper PSW-37. 5 p.

Lamb, W.H. 1937. Virginia trees. Vol. I: The conifers. Manassas Journal Press, Manassas, Virginia. 112 p.

Lambert, A.B. 1803. A description of the genus Pinus, illustrated with figures, directions relative to the cultivation, and remarks on the uses of the several species. T. Bensley, London.

_____. 1805. On a new species of Pinus. Ann. Bot. 2: 198-199.

Lanjouw, J., and F.A. Stafleu. 1964. Index herbariorum. Part I. The herbaria of the world. Regnum Vegetabile, vol. 31. 251 p.

Ledig, F.T., and T.O. Perry. 1965. Physiological genetics of the shoot-root ratio. Proc. Soc. Amer. Foresters (1965): 39-43.

Legrand, H.E. 1960. Geology and ground-water resources of Pittsylvania and Halifax Counties. Virginia Div. Mineral Resources Bull. 75. 86 p.

Liddicoet, A.R., and F.I. Righter. 1960. Trees of the Eddy Arboretum. Pacific Southwest Forest and Range Exp. Sta. Misc. Paper 43.

Liming, F.G. 1957. Homemade dendrometers. J. Forestry 55: 575-577.

Little, E.L., Jr., S. Little, and W.T. Doolittle. 1967. Natural hybrids among pond, loblolly and pitch pines. Northeastern Forest Exp. Sta., U.S. Forest Service Res. Paper NE-67. 22 p.

Little, S. 1964. Fire ecology and forest management in the New Jersey pine region. Proc. 3rd Annu. Tall Timbers Fire Ecol. Conf.: 34-59.

Little, S., and F. Mergen. 1966. External and internal changes associated with basal-crook formation in pitch and shortleaf pines. Forest Sci. 12: 268-275.

Losche, C.K. 1967. Soil genesis and forest growth on steeply sloping landscapes of the southern Appalachians. Ph.D. Diss., N.C. State Univ. 177 p.

Loudon, J.C. 1844. Arboretum et fruticetum Britannicum, 2nd Ed., Vol. 4 Text. London.

McIntyre, A.C. 1929. A cone and seed study of the mountain pine (Pinus pungens Lambert). Amer. J. Bot. 16: 402-406.

Marx, D.H., and C.B. Davey. 1967. Ectotrophic mycorrhizae as deterrents to pathogenic root infections. Nature 213: 1139.

Mason, H.L., and P.R. Stout. 1954. The role of plant physiology in plant geography. Annu. Rev. Plant Physiol. 5: 249-270.

Maull, T.W. 1963. Seed germination and establishment of Pinus rigida Miller (an autecological study). Ph.D. Diss., Penn. State Univ. Diss. Abstr. 23: 3607-3608.

Meehan, T. 1889. Note on Pinus pungens and its allies. Contributions to the life histories of plants, no. 4. Proc. Acad. Natur. Sci., Philadelphia, March 26, 1889: 56-58.

Michaux, A. 1889. Journal de Andre Michaux, 1787-1796. Proc. Amer. Phil. Soc. 26: 8-145.

Michaux, F.A. 1810. Histoire des arbres forestiers de l'Amerique Septentrionale... Vol. I. L. Haussmann et d'Hautel, Paris.

_____. 1819. The North American Sylva. Vol. 3. C. d'Hautel, Paris. 285 p.

Mirov, N.T. 1967. The genus Pinus. Ronald Press, New York. 602 p.

Mollenhaur, W., Jr. 1939. Table Mountain pine--squirrel food or timber tree? J. Forestry 37: 420-421.

Monk, C.D. 1966a. Root-shoot dry weights in loblolly pine. Bot. Gaz. 127: 246-248.

_____. 1966b. An ecological significance of evergreenness. Ecology 47: 504-505.

Mowbray, T.B. 1967. Vegetational gradients in relation to environment and phenology in a southern Blue Ridge gorge. Ph.D. Diss., Duke Univ. 300 p.

Murphy, T.D. A table of vapor pressure deficits for relative humidities of 10%-100% and temperatures of 0°-121°F. Mimeogr., Dep. Zool., Duke Univ., Durham, N.C. 14 p.

Nelson, W.A. 1962. Geology and mineral resources of Albemarle County. Virginia Div. Mineral Resources Bull. 77. 92 p.

North Carolina Department of Conservation and Development, Division of Mineral Resources. 1958. Geologic map of North Carolina.

Nuttall, T. 1857. The North American Sylva; or, a description of the forest trees of the United States, Canada, and Nova Scotia, not described in the work of F. Andrew Michaux. Vol. 2. D. Rice and A.N. Hart, Philadelphia.

Oosting, H.J. 1948. Ecological notes on the flora of east Greenland and Jan Mayen, In Boyd, Louise A., and others. The coast of northeast Greenland. Amer. Geogr. Soc. Spec. Pub. 30. New York.

_____. 1956. The study of plant communities. 2nd ed. W.H. Freeman and Co., San Francisco. 440 p.

Parker, J. 1952. Environment and forest distribution of the Palouse Range in northern Idaho. Ecology 33: 451-461.

Pennsylvania Department of Internal Affairs. 1960. Geologic map of Pennsylvania, 1:250,000.

Perry, T.O., and G.W. Baldwin. 1966. Winter breakdown of the photosynthetic apparatus of evergreen species. Forest Sci. 12: 298-300.

_____, Wang Chi-Wu, and D. Schmitt. 1966. Height growth for loblolly pine provenances in relation to photoperiod and growing season. Silvae Genet. 15: 61-64.

Phillips, E.A. 1959. Methods of vegetation study. Henry Holt and Co., Inc. 107 p.

Pinchot, G., and W.W. Ashe. 1897. Timber trees and forests of North Carolina. North Carolina Geol. Surv. Bull. 6.

Price, P.H., and E.T. Heck. 1939. West Virginia Geological Survey: Greenbrier County. 846 p.

Racine, C.H. 1966. Pine communities and their site characteristics in the Blue Ridge escarpment. J. Elisha Mitchell Sci. Soc. 82: 172-181.

Rand, Patricia J. 1965. Factors related to the distribution of ponderosa and pinyon pines at Grand Canyon, Arizona. Ph.D. Diss., Duke Univ. 311 p.

Reed, John C., Jr. 1964. Geology of the Linville Falls Quadrangle, North Carolina. U.S. Geol. Surv. Bull. 1161-B. 53 p.

Reid, P.H., and Carolyn Copeland. 1966. Tentative analytical methods used for the testing of farmers samples by the Soil Testing Division, North Carolina Department of Agriculture, Raleigh, North Carolina, as of April 1, 1966. Mimeogr. 15 p.

Reiners, W.A. 1965. Ecology of a heath-shrub synusia in the pine barrens of Long Island, New York. Torrey Bot. Club Bull. 92: 448-464.

_____. 1967. Relationships between vegetational strata in the pine barrens of central Long Island, New York. Torrey Bot. Club Bull. 94: 87-99.

Reinhart, K.G. 1961. The problem of stones in soil-moisture measurement. Proc. Soil Sci. Soc. Amer. 25: 268-270.

Richards, B.N. 1965. Mycorrhiza development of loblolly pine seedlings in relation to soil reaction and the supply of nitrate. Plant and Soil 22: 187-199.

_____ and G.K. Voigt. 1964. Role of mycorrhiza in nitrogen fixation. Nature 201: 310-311.

Richards, L.A. 1965. Water retentivity of soil at specified values of matric suction. p. 131-137 In Black, C.A. (ed.). Methods of soil analysis. Part 1. Physical and mineralogical properties, including statistics of measurement and sampling. Agronomy, No. 9. Amer. Soc. Agron., Inc., Madison. 770 p.

Richards, L.A., and G. Ogata. 1958. Thermocouple for vapor pressure measurement in biological and soil systems at high humidity. Science 128: 1089-1090.

Righter, F.I. 1939. Early flower production among the pines. J. Forestry 37: 935-938.

Rodgers, C.L. 1965. The vegetation of Horsepasture Gorge. J. Elisha Mitchell Sci. Soc. 81: 103-111.

Ruby, J.L. 1967. The correspondence between genetic, morphological and climatic variation patterns in Scotch pine. I. Variations in parental characters. Silvae Genet. 16: 50-56.

Sargent, C.S. 1897. The silva of North America. Vol. 11: Coniferae (Pinus). Houghton, Mifflin and Co., Boston. 160 p.

Shaw, G.R. 1914. The genus Pinus. Pub. Arnold Arboretum 5. Riverside Press, Cambridge, Mass. 96 p.

Slatyer, R.O. 1967. Plant-water relationships. Academic Press, London. 366 p.

Slocum, G.K., and W.D. Miller. 1953. Virginia pine: Reproduction, growth and management on the Hill Demonstration Forest, Durham County, N.C. North Carolina Agr. Exp. Sta. Tech. Bull. 100. 52 p.

Smith, C.C. 1965. Interspecific competition in the genus of tree squirrels Tamiasciurus. Ph.D. Diss., Univ. Washington, Zool. Dep. 269 p.

Spalt, K.W., and W.E. Reifsnyder. 1962. Bark characteristics and fire resistance: A literature survey. Southern Forest Exp. Sta. Occasional Paper 193. 19 p.

Steel, R.G.D., and J.H. Torrie. 1960. Principles and procedures of statistics with special reference to the biological sciences. McGraw-Hill Book Co., New York. 481 p.

Stone, E.L., Jr., and M.H. Stone. 1943. Dormant buds in certain species of Pinus. Amer. J. Bot. 30: 346-351.

_____ and _____. 1954. Root collar sprouts in pine. J. Forestry 52: 487-491.

Stupka, A. 1964. Trees, shrubs and woody vines of Great Smoky Mountains National Park. Univ. Tennessee Press, Knoxville. 186 p.

Sudworth, G.B. 1913. Geographic distribution of North American trees. Part I: Pines. U.S. Dep. Agr., Forest Service.

Tamm, C.O. 1964. Determination of nutrient requirements of forest stands. Int. Rev. Forestry Res. 1: 115-170.

Tatnall, R.R. 1946. Flora of Delaware and the eastern shore. Soc. Natur. Hist. Delaware. 313 p.

Tilton, J.L., W.F. Prouty and P.H. Price. 1927. West Virginia Geological Survey: Pendleton County. 384 p.

Tranquillini, W. 1965. Uber den Zusammenhang zwischen Entwicklungzustand und Durreresistenz junger Zirben (Pinus cembra L.) im Planzgarten. (On the connection between developmental stage and drought resistance of young Cembran pine (Pinus cembra L.) in the nursery.) Beitr. Subalpinen Waldforsch. 66: 243-271. (Eng. summary).

Trappe, J.M. 1967. Principles of classifying ectotrophic mycorrhizae for identification of fungal symbionts. 14th Congr. Int. Union Forest Res. Organ. Proc.: 46-59.

U.S. Department of Agriculture, Bureau of Chemistry and Soils. Soil Survey, Series 1926 (no. 22), 1930 (no. 14), 1932 (no. 13, 20, 31).

U.S. Department of Agriculture, Bureau of Plant Industry. Soil Survey, Series 1934 (no. 20, 27), 1937 (no. 3, 9).

U.S. Department of Agriculture, Bureau of Soils. Report of Field Operations No. 8, 14, 17, 23.

U.S. Department of Agriculture, Forest Service. 1948. Woody plant seed manual. U.S. Dep. Agr. Misc. Pub. 654. 416 p.

U.S. Department of Agriculture, Soil Conservation Service. Soil Survey, Series 1938 (no. 16), 1940 (no. 15), 1942 (no. 6), 1944 (no. 2, 6), 1945 (no. 1), 1946 (no. 1), 1956 (no. 4, 15), 1958 (no. 7), 1959 (no. 27).

U.S. Department of Commerce, Weather Bureau. 1960. Climates of the States: Pennsylvania. Climatography of the United States No. 60-36.

U.S. Department of the Interior, Geological Survey. Geological atlas of the United States. Folio No. 14, 32, 61, 147, 170.

Virginia Division of Mineral Resources. 1963. Geologic map of Virginia.

Vokes, H.E. 1957. Geography and geology of Maryland. Maryland Dep. Geol., Mines and Water Resources, Bull. 19. 243 p.

Ward, L.F. 1877. Pinus pungens in the District of Columbia. Field and Forest 3(3): 53. Reprinted in Ward, L.F. 1913. Glimpses of the Cosmos. Vol. 2, p. 146-147. G.P. Putnam's Sons, New York.

Watt, A.S. 1950. Contributions to the ecology of bracken (Pteridium aquilinum). V. Bracken and frost. New Phytol. 49: 308-327.

Wells, O.O., and P.C. Wakeley. 1966. Geographic variation in survival, growth, and fusiform-rust infection of planted loblolly pine. Forest Sci. Monogr. 11. 40 p.

Whitehead, D.R. 1964. Fossil pine pollen and full-glacial vegetation in southeastern North Carolina. Ecol. 45: 767-777.

Whitmore, F.W., and R. Zahner. 1967. Evidence for a direct effect of water stress on tracheid cell wall metabolism in pine. Forest Sci. 13: 397-400.

Whittaker, R.H. 1956. Vegetation of the Great Smoky Mountains. Ecol. Monogr. 26: 1-80.

Wiersma, J.H. 1963. A new method of dealing with results of provenance tests. Silvae Genet. 12: 200-205.

Williams, E.J. 1959. Regression analysis. John Wiley and Sons, Inc., New York. 214 p.

Williams, Ruby M., and H.J. Oosting. 1944. The vegetation of Pilot Mountain, North Carolina: A community analysis. Torrey Bot. Club Bull. 71: 23-45.

Woodwell, G.M. 1958. Factors limiting growth of pond pine seedlings in organic soils of the Carolinas. Ph.D. Diss., Duke Univ. 87 p.

Wright, R.D. 1966. Lower elevational limits of montane trees: I. Vegetational and environmental survey in the San Bernardino Mountains of California. Bot. Gaz. 127: 184-193.

_____. 1967. CO_2 exchange rates of conifers in relation to their elevational range. Amer. Inst. Biol. Sci., Annu. Meeting, August, 1967.

BIOGRAPHY

Name: Donald Bruce Zobel

Birth: July 17, 1942; Salinas, California

Education: North Carolina State College, B.S., 1964

Duke University, A.M., 1966

Awards: National Aeronautics and Space Administration Traineeship, 1964-1967

National Science Foundation Graduate Fellowship, 1967-1968

Societies: Ecological Society of America

Society of American Foresters

American Association for the Advancement of Science